Report.

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

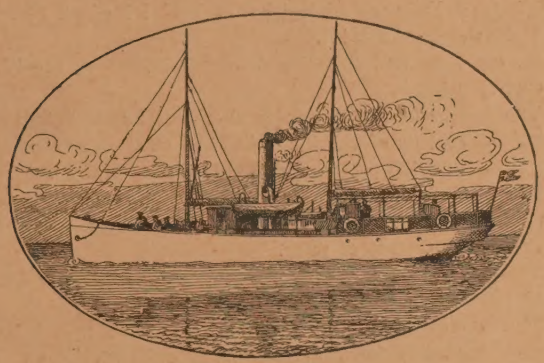
Report

of

The Danish Biological Station

to

The Board of Agriculture.



XXXIII.

1927.

By

A. C. Johansen,
Dr. phil.
Director.

Copenhagen.
In Commission by G. E. C. Gad.
Centraltrykkeriet.
1927.

The Reports from The Danish Biological Station (Nos. I—XXI) are published in the official Danish "Fiskeri-Beretning" for the years 1890—91 until 1912. After this year they appear as special publications. The Reports I—XXXII are edited by C. G. Joh. Petersen, Ph. D., L. L. D., D. Sc.

I. *C. G. Joh. Petersen*: Fiskenes biologiske Forhold i Holbæk Fjord. (1890—91)*) 63 pp. 1 Chart. Out of print.

II. *The same*: On the Eggs and Breeding of our Gobiidæ. (1891—92.) 9 pp. Two Plates. Out of print.

III. *The same*: The Pelagic Life in Fænø Sound etc. (1892—93.) 38 pp. Tables. Out of print.

IV. *The same*: On the Biology of our Flat-fishes and on the decrease of our Flat-fish Fisheries. (1893—94.) 146 pp. 2 Plates. 1 Chart. Many Tables. Out of print.

V. *The same*: The common Eel (*Anguilla vulgaris* T.) gets a Particular Breeding-dress before its Emigration to the Sea. (1894—95.) 35 pp. With 2 Plates. Etc. 64 pp. Out of print.

VI. *The same*: The Yearly Immigration of young Plaice into the Limfjord etc. (1895—96.) 48 pp. 1 Chart. 2 Tables. Out of print.

VII. *The same*: Plankton-Studies in the Limfjord. 1897. 23 pp. 1 Map. 4 Tables.

VIII. *The same*: An Otter-Seine for the Exploration of Deeper Seas. 1898. 24 pp. With 10 Figures. Out of print.

IX. *The same*: Trawlings in the Skager Rack and the Northern Cattegat in 1897 and 98. 1899. 56 pp. With one Map. Out of print.

X. *The same*: List of The "Aalerusestader" in Denmark, etc. — Smaller Communications. 1899 and 1900. 37 pp.

XI. *The same*: I. The Biology of the Cod in the Danish Seas. II. On other Codfishes in our Seas. III. Some General Observations on Protection, Legislation etc. IV. Alterations and Improvements on Otter-seines for Zoological Purposes. 1900 and 1901. 44 pp.

XII. *The same*: I. Where, and under what Conditions, can the Eggs of Plaice be developed into Young Fish within the Skaw? II. On the Young Stages of the genus *Zeugopterus*. (With one Plate.) III. Can we enter into Competition with the Foreign Steam-trawlers in our Seas outside the Danish Territorial Limit. 1902 and 1903. 33 pp.

XIII. *A. Otterstrøm*: Eggs and Young of Fishes in the Danish Waters. (Investigations during 1904 and earlier years.) 1903 and 1904. 85 pp.

XIV. *C. G. Joh. Petersen*: I. The Influence of Light on the Migrations of the Eel. II. *K. I. Gemzøe*: Age and Rate of Growth of the Eel. 1906. 39 pp.

XV. *C. G. Joh. Petersen*: I. First Report on the Oysters and Oyster Fisheries in the Lim Fjord. (70 pp.) 1908.

XVI. *C. H. Ostenfeld*: On the Ecology and Distribution of the Grass Wrack (*Zostera marina*) in Danish Waters. With 9 figures. 1908. 62 pp.

---

*) The figures in ( ) refer to the "Fiskeri-Beretning" for the years quoted.

Report

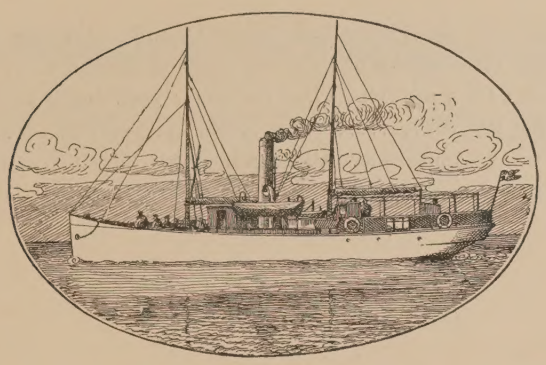
LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

of

The Danish Biological Station

to

The Board of Agriculture.



XXXIII.

1927.

By

A. C. Johansen,
Dr. phil.
Director.

Copenhagen.
In Commission by G. E. C. Gad.
Centraltrykkeriet.
1927.

CONTENTS.

Page

I. A. C. Johansen: On the Fluctuations in the Quantity of Young Fry among Plaice and certain other species of fish, and causes of the same 3

II. A. C. Johansen: On a Spawning Place for winter spawning Herring in the northern part of the Belt Sea 17

III. H. Blegvad: On the Annual Fluctuations in the Age-composition of the Stock of Plaice. 25

IV. R. Spärck: Studies on the Biology of the Oyster *(Ostrea edulis)* II-IV 43

I.

On the Fluctuations in the Quantity of Young Fry among Plaice and certain other species of fish, and causes of the same.

The fishing experiments carried out by Apstein[1]) on the shores of the Kiel Bay in 1893—99 showed that the quantity of young fry of the plaice, the 0-group, varied considerably from year to year, and the researches of C. G. Joh. Petersen have shown that such variations in the quantity of young fry were also discernible in the southern part of the Belt Sea, near the Danish shores. In Report XII from the Danish Biological Station for 1904, Dr. Petersen states inter alia: that in the year 1893 there were, practically speaking, no young plaice of the 0-group in the southern waters of the Belt Sea (i. e. south of a line from Snoghøj via the northern extremity of Langeland to Korsør), whereas in 1902 there was a fairly numerous stock of 0-group plaice in this area. Investigations of this nature were soon afterwards instituted also in the case of other fishes. Knut Dahl[2]) for instance made, in 1903—06, a series of fishing experiments with the seine in some of the fjords on the southern coast of Norway, in order to procure information as to the frequency of cod fry in the bottom stage. These experiments showed that in the fjords investigated (Søndeledfjord, Hellefjord, Sandnæsfjord etc.) there was a greater quantity of young fry in 1904 than in 1905, while both these years were probably far in excess of 1903 as regards the quantity of young fry.

The earliest fishing experiments made for the study of variation in the quantity of young fish were not carried out with a very high degree of precision, but in course of time, investigators recognised the necessity of using uniform implements in the different years, and of introducing a so called fishing unit, that is, the employment of uniform implements for a given time or over a given range of ground. In 1904 for instance, the Danish Biological Station introduced, as a fishing unit for the 0-gr. plaice, the use of a hand shove net for a distance of 50 metres; the Danish Commission for Investigation of the Sea adopted, in 1905, as fishing unit for 0-gr. plaice, the catch per hour made with a small fine-meshed plaice trawl with otter boards.

---

[1]) C. Apstein: Junge Butt (Schollen, Pleuronectes platessa) in der Ostsee. — Wiss. Meeresunters. N, F. VIII Bd. Abt. Kiel 1904.

[2]) Aarsberetning vedkommende Norges Fiskerier for 1906. 1. Hefte.

Long before this, at the beginning of the 80's, Professor Hensen[1]) of Kiel, had constructed his famous net for quantitative determination of plankton in the sea, including pelagic fish eggs and the tiny pelagic stages of the young fish. This implement is to this day the best for quantitative determination of fish eggs, but in the case of pelagic fry it is as a rule too small. In fishing experiments for the capture of pelagic fry it is now customary to use large bag-shaped implements made of stramin such as the Petersen young-fish-trawl and the ring-trawl. These implements are used either for horizontal hauls at various depths, or are drawn up through the different water layers from bottom to surface.

By means of fishing experiments with such implements as these, we have ascertained that the Danish and adjacent waters exhibit great fluctuations from year to year in the quantity of young fry of several species, such as the cod, haddock, plaice, herring etc.

When the method introduced by Hoffbauer and Reibisch of determining the age of fish by means of the rings in their scales or otoliths had become generally accepted, it was found that age analyses of older specimens confirmed the information obtained by fishing experiments as to the fluctuations in the quantity of young fish from year to year. Particularly well known are Lea's investigations among the Norwegian spring herring, showing that a single year-class of these fish could dominate the catches made on the coasts of Norway throughout a long series of years.

The existence of great fluctuations in the quantity of young fish from year to year has thus been demonstrated as a fact in the case of several of our species of fish, and this in several different ways; and in course of time, it was realised that the great fluctuations in the yield of the fisheries by weight could as a rule be explained as due to more or less favourable survival years for the young fish some years before the fishery for the marketable fish took place.

As regards the Causes of the Fluctuations, attention is naturally directed to the following points:

1) Variations in the number of spawning fish or in the number of fish eggs from year to year.
2) More or less favourable external conditions for the development of the young (favourable temperature, suitable salinity, abundance of oxygen etc.).
3) More or less favourable conditions as to nourishment for the tiny larvae.
4) The presence in more or less considerable numbers of such organisms as prey upon the fish eggs or young fry.

We will now proceed to consider each of these possible items separately, as possible causes of the fluctuations in the number of young fry.

---

[1]) Hensen: Ueber die Bestimmung des Planktons oder des im Meere treibenden Materials an Pflanzen und Thieren. Fünfter Bericht der Kommission zur wiss. Unters. d. deutschen Meere. Kiel. Berlin 1887.

As regards the variation in numbers of spawning fish or of fish eggs, there are various points which suggest that this factor cannot be the principal cause of the fluctuations in the quantity of young fish. I may point out for instance, that during the period 1893—1904, when the stock of plaice in the Belt Sea and southern Kattegat was not as yet greatly affected by the fishery, and when the numbers of spawning fish cannot have varied to any great extremes from year to year, there were nevertheless enormous fluctuations in the numbers of young fry. I would also quote a fact noted by Dr. Hjort[1]) with regard to the cod, viz. that in 1904, when remarkably large numbers of cod fry were developed on the coast of Norway, the quantity of roe in the Lofoten cod was unusually small.

We cannot, however, conclude from this that the amount of ova produced should be altogether without influence on the fluctuations in the quantity of young fry. It has been shown, in the case of the salmon in the Gudenaa[2]) that there is a rhythmic movement of the yield embracing a period of 5—6 years, answering to the time elapsing between the entry of a winter salmon into the Gudenaa and the entry of its offspring into the same river. After a year with a good yield there will, normally, be another good yield 5 or 6 years later. Now the salmon produces but relatively few eggs, and these are not shed in the sea; it has been shown recently, however, by Aage Jensen[3]) that there is a rhythmic movement in the yield of the Bornholm herring fishery with a period of 3—4 years, suggesting that the number of spawning herring counts for something in the fluctuations in the production of young. The herring of the Bornholm waters generally attain maturity at an age of 3 years.

As regards the more or less favourable external conditions for the development of the young fry, this is a factor naturally cited in seeking to explain the fluctuations in question and I will here set forth in some detail what is known as to the relationship between fluctuations in the quantity of young fry among the plaice of the Southern Kattegat and the Belt Sea on the one hand, and fluctuations of temperature and salinity during the main spawning season of the plaice, — January and February — on the other.

In the Southern Kattegat and the Belt Sea, systematic investigations have been made by the Danish Commission for Investigation of the Sea with regard to fluctuations in the frequency of young plaice from year to year. The experiments were made with a small fine meshed young-fish-trawl, having a ground

---

[1]) Johan Hjort: Fluctuations in the great Fisheries of Northern Europe. Rapports et Procès-Verbaux. Cons. perm. internat. Vol. XX. Copenhague 1921.

[2]) J. P. Jacobsen and A. C. Johansen: On the causes of the fluctuations in the yield of some of our fisheries. I. Medd. Komm. f. Havundersøgelser Ser. Fiskeri. Bd. VI No. 5. København 1921.

[3]) Aage J. C. Jensen: On the Influence of the Quantity of Spawning Herrings upon the Stock of the following years. Journal du Conseil. vol. II. No. 1 1927.

line 7 m. long[1]), on sandy bottom close to shore, as a rule at depths from 1—3 m. where the 0-gr. fish are most frequently found and those of the I-gr. also fairly numerous. Fishing experiments of this sort have been carried out every year since 1905, save for an interruption as the consequence of the great war, from 1915—1919, and we have thus a considerable amount of material available to throw light on the fluctuations in question.

In the Southern Kattegat and Belt Sea, the stock of 0-gr. plaice belong to

Table 1. Number of plaice of 0- and I-group.

Captured with fine meshed young plaice trawl per hour in the southern Kattegat and Belt Sea (Number of stations in brackets).

Year	Southern Kattegat[2])		Belt-Sea[3])		Southern Kattegat and Belt-Sea		Relative values deduced therefrom
	0-gr.	I-gr.	0-gr.	I-gr.	0-gr.	I-gr.	1 × 0-gr. + 3 × I-gr.
1904	— (0)	— (0)	— (0)	— (0)	— (0)	— (0)	2.4
1905	11.1 (14)	0.7 (14)	10.4 (8)	0.0 (8)	10.9 (22)	0.4 (22)	24.1
1906	20.7 (13)	2.5 (13)	23.9 (7)	7.9 (7)	21.8 (20)	4.4 (20)	61.4
1907	6.0 (1)	13.2 (6)	— (0)	— (0)	6.0 (1)	13.2 (6)	12.0
1908	23.7 (3)[4])	— (0)	44.0 (9)[4])	— (0)	38.9 (12)	— (0)	61.7
1909	1.9 (27)	5.6 (27)	6.0 (5)	18.6 (5)	2.6 (32)	7.6 (32)	10.1
1910	3.2 (26)	2.5 (26)	— (0)	— (0)	3.2 (26)	2.5 (26)	7.7
1911	74.6 (34)	1.0 (34)	48.4 (35)	2.0 (35)	61.3 (69)	1.5 (69)	97.0
1912	7.4 (36)	9.4 (36)	2.7 (41)	14.0 (41)	4.9 (77)	11.9 (77)	16.9
1913	11.4 (26)	4.3 (26)	19.0 (2)	0.0 (2)	11.9 (28)	4.0 (28)	39.8
1914	1.5 (4)	36.8 (4)	6.1 (21)	4.1 (21)	5.4 (25)	9.3 (25)	10.8
1919	— (0)	— (0)	— (0)	— (0)	— (0)	— (0)	19.8
1920	58.0 (3)	3.3 (3)	— (0)	— (0)	58.0 (3)	3.3 (3)	73.3
1921	1.5 (30)	3.6 (30)	5.4 (35)	6.4 (35)	3.6 (65)	5.1 (65)	27.6
1922	1.0 (22)	6.7 (27)	16.9 (43)	8.7 (43)	11.5 (65)	7.9 (70)	23.0
1923	— (0)	— (0)	— (0)	— (0)	— (0)	— (0)	46.8
1924	15.5 (30)	5.1 (30)	18.4 (38)	10.0 (38)	17.1 (68)	7.8 (68)	32.7
1925	— (0)	— (0)	22.8 (33)	5.2 (33)	22.8 (33)	5.2 (33)	49.8
1926	— (0)	— (0)	3.9 (28)	9.0 (28)	3.9 (28)	9.0 (28)	7.8
Mean					17.7	6.2	32.9

[1]) The trawl is described by A. C. Johansen in "Fünfter Bericht über die Pleuronectiden in der Ostsee". Rapports et Procès-Verbaux. Conseil perm. internat. vol. XXII. 1915.

[2]) Northern limit: A line from Als Odde (Mariager Fjord) — Anholt Knob Light vessel — Tylø Light.

[3]) Southern limit: A line from Kjels Nor Light to Kappel Church (Laaland), and a line from Skjoldnæs Light to Pøls Huk.

[4]) Captured as I-Gr. in April 1909.

the Baltic Race, without any noteworthy intermixture of young fish that have grown up in the North Sea and Skagerak. The northern limit of the area we are now considering runs from Als Odde (Mariager Fjord) north of Anholt Knob Lightship and thence to Tylö Light in Halland. The southern boundary lies in the Sound, along the line Dragør-Limhamn. The Western Baltic is here not included in the Belt Sea.

The experiments showed that, in the area here in question, the 0-gr. fish were taken, on an average, in three times as great numbers as the I-gr. reckoned per station and per hour.

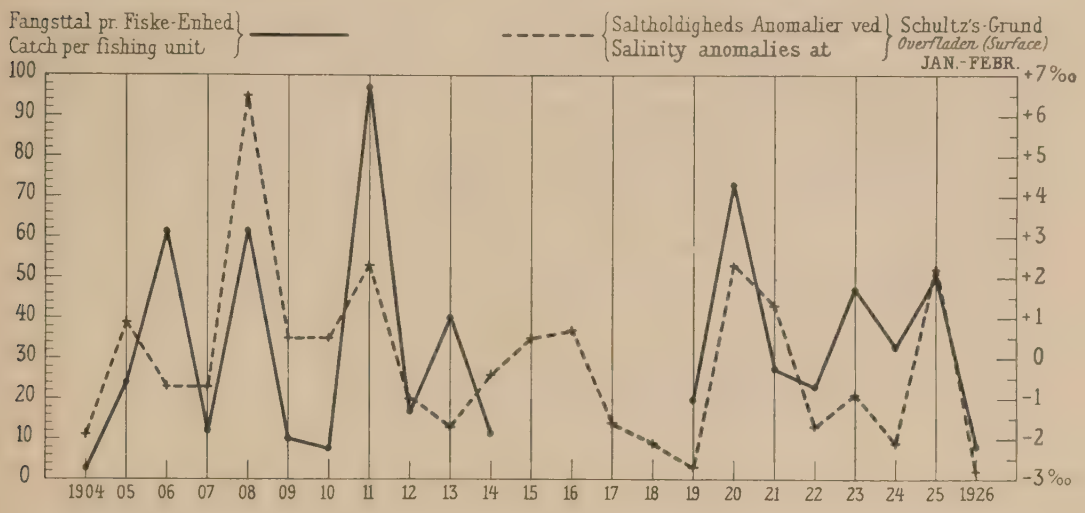


Fig. 1. Variation in the catch per hour of young plaice of 0-Gr. etc. in the Southern Kattegat and Belt Sea, compared with deviations from mean salinity of surface water at Schultz's Grund Lightship during the years 1904—1926. (For the fishing gear and the calculation of the catch figures see p. 7—9).

Table 1 shows the average hauls of plaice of the 0-gr. and I-gr. in the Southern Kattegat and Belt Sea during the period covered by the experiments. The catch figures are reckoned as follows: The average catch of 0-gr. plaice per hour is taken for a given year, plus three times the catch of the I-gr. in the following year. This gives an expression for the catch of the same year-class in two successive years. Where only information as to the catch of the 0-gr. is available for a given year, and none as to the catch of the I-gr. in the following year, the number of specimens of the 0-gr. is multiplied by two, so as to render the figure comparable with the figure above mentioned. Finally, where only information as to the catch of the I-gr. is available, the number of specimens is multiplied by 6, to render it comparable with the rest.

It will be seen from Table 1, that the highest figure for the period 1904—1926 falls in 1911 and the lowest in 1904. The catch figures are, 97.0 for 1911 and only 2.4 for 1904. As the mean of all the values we have the figure 32.9.

Fig. 1 shows the fluctuations in the quantity of young fry compared with fluctuations in the surface salinity at Schultz's Grund Lightship, which lies in the middle of the area here considered.

The figure shows that the years 1906, 1908, 1911, 1920, 1923 and 1925 have relatively high catch figures, while those for 1904, 1907, 1909, 1910, 1912, 1914, 1919, 1922 and 1926 are relatively low: the values for 1905, 1913, 1921 and 1924 are not far from the average. If we now compare the curve for these values with that representing salinity anomalies of the surface water at Schultz's Grund Lightship in January—February, we find a distinct agreement in their courses. Years with low catch values have on the whole low salinity in the upper water layers during January-February, i. e. during the months which constitute the main spawning period of the plaice in the area in question. On calculating the correlation coefficient between the catch figures and the salinity anomalies, we obtain $r = + 0.57$ and $\sigma_r = 0.15$. The correlation coefficient is thus about four times as great as the mean error of the same, and the connection between fluctuations and salinity must thus be regarded as an established fact.

Calculating the correlation between catch figures and salinity for the separate months, we obtain:

For January: $r = + 0.48$; $\sigma_r = 0.18$.
For February: $r = + 0.55$; $\sigma_r = 0.17$.
For March: $r = + 0.02$; $\sigma_r = 0.24$.

From this it would seem that the salinity in January and February affects the quantity of young fry, whereas it is doubtful whether the salinity in March has any such effect.

Fig. 2 shows the catch of young fry of the plaice for the different years compared with the surface temperature at Schultz's Grund Lightship, and it will be seen that we have here also a certain agreement between the courses of the two curves. In years with relatively low temperature during January-February, the catch figures are also below the normal. On calculating the correlation coefficient for Jan.—Feb., we obtain $r = 0.31$ and $\sigma_r = 0.21$. Calculating the correlation coefficient for the different months, we obtain:

For January: $r = + 0.19$; $\sigma_r = 0.22$.
For February: $r = + 0.33$; $\sigma_r = 0.21$.
For March: $r = + 0.20$; $\sigma_r = 0.22$.

The correlation coefficient for February is here about 1.5 times as great as the mean error of the same, and as the coefficients for January and March are also positive, the connection betwen catch and temperature seems to be a reality.

An indication of this connection between the winter temperature and the numbers of young plaice developed in the year in question is also found in Fig. 3, where the catch figures for young fry of the plaice are compared with the number

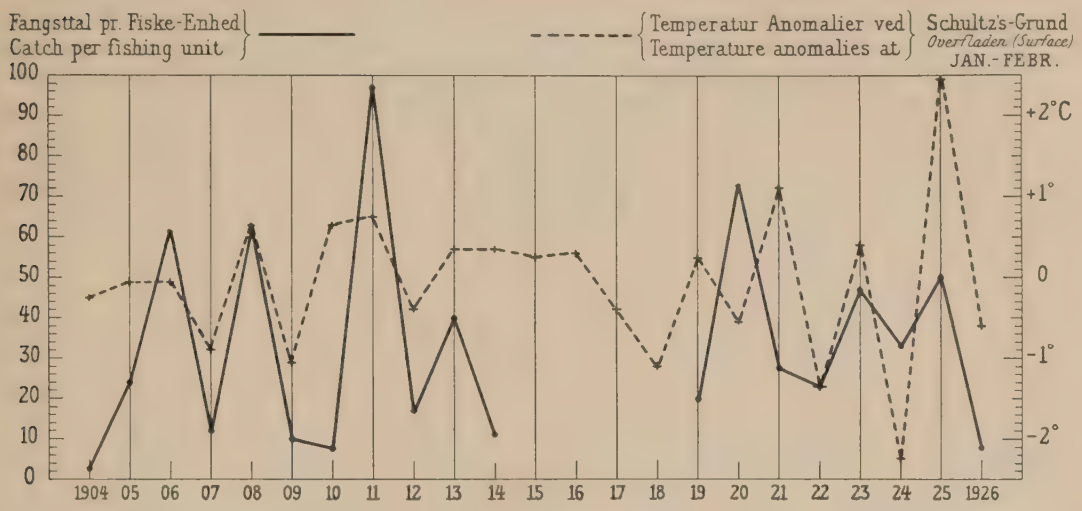


Fig. 2. Variation in the catch per hour of young plaice of 0-Gr. etc. in the Southern Kattegat and Belt Sea compared with deviations from mean temperature of surface water at Schultz's Grund Lightship during the years 1904—1926. (For the fishing gear and the calculation of the catch figures see p. 7—9).

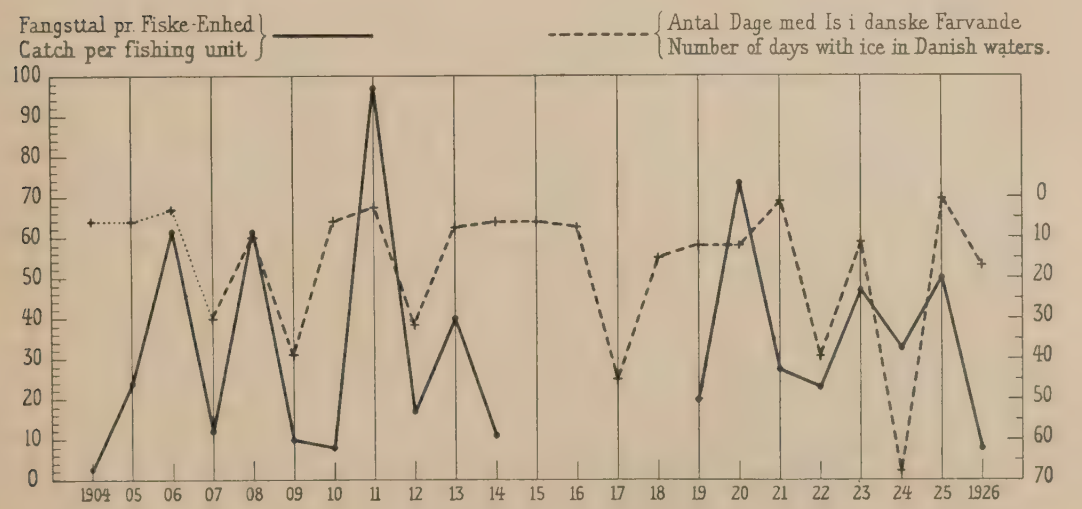

Fangsttal pr. Fiske-Enhed
Catch per fishing unit
Antal Dage med Is i danske Farvande
Number of days with ice in Danish waters.
1904 05 06 07 08 09 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 1926

Fig. 3. Variation in the catch per hour of young plaice of 0-Gr. etc. in the Southern Kattegat and Belt Sea compared with the numbers of days when ice was recorded in the Danish waters (For the fishing gear and the calculation of the catch figures see p. 7—9).

of days on which ice was observed in Danish waters. On calculating the correlation coefficient for the two sets of values, we obtain:

$$r = \div 0.27; \ \sigma_r = 0.21.$$

During the years when we have had severe or fairly severe ice winters, such as 1907, 1909, 1912, 1922 and 1924, the catches are only small, or at best of medium size. We know also, that after the severe ice winters of 1893 and 1900, only very small quantities of plaice fry appeared.

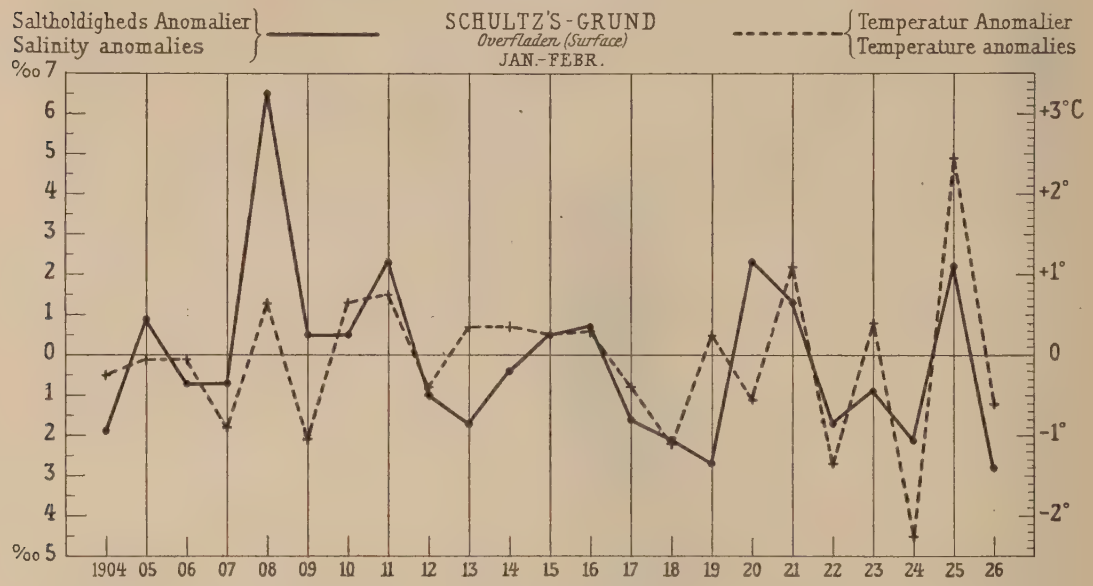


Fig. 4. Comparison between salinity anomalies and temperature anomalies of the surface water at Schultz's Grund Lightship for the years 1904—1926.

That there exists a certain connection, again, between low salinity and low temperature is apparent from Fig. 4, and it is easy to understand that such must be the case. In cold winters, the easterly winds prevail to a relatively considerable extent and these easterly winds bring comparatively large quantities of the less salt water from the Baltic out through the Belts and the Kattegat.

During periods when the water has been covered with ice for a long time, the quantity of oxygen in solution in the water will be reduced, which undoubtedly occasions a rise in the mortality percentage of eggs and tiny larval stages; it should be noted however, that when the temperature of the water falls to about 0° C. or below this, the amount of oxygen consumed by eggs and larvæ is very slight.

The investigations made indicate very definitely that both salinity and temperature during the winter season exercise a perceptible influence upon the numbers of young plaice appearing on the coast in the year in question. This suggests that the fishing experiments with the fine meshed plaice-trawl on the coasts have

yielded results of essential importance, despite the fact that in many of the years included they were by no means carried out to the extent which I could have wished. — One is tempted to assume that if investigations had been carried out each year on the same scale as in 1911, 1912, 1921, 1922 and 1924[1]) the connection between catch figures on the one hand and temperature and salinity on the other would have been even more distinctly apparent. I should add that, in so far as comprehensive age analyses of the grown up plaice have been made in the Southern Kattegat and Belt Sea, these have confirmed the results of the coast investigations as regards more or less favourable survival years for the young fry. This applies also to the period 1921—25, for which period Dr. Blegvad has, by age analyses of the adolescent fish, found the same fluctuations as I have observed in the coast investigations. (See this Report No. III).

The question now arises: Is the influence of winter salinity and temperature on the quantity of young fry to be regarded as direct, or is it merely indirect, acting through its effect on the amount of nourishment available for the tiny larvæ?

As regards salinity, the effect might very well be direct, as a considerable number of pelagic eggs of the plaice in the shallower parts of the Belt Sea and Kattegat can, during periods of low salinity, sink down to the bottom, where they would fall an easy prey to the numerous predatory creatures of the sea floor. The specific gravity of the pelagic ova can no doubt to a certain extent adapt itself to that of the water[2]), but the change takes time, whereas the egg sinks rapidly as soon as the specific gravity of the water becomes too low. Throughout extensive areas however, the eggs will only sink down to the lower and salter water layers, when a marked inflow of relatively fresh Baltic water takes place.

It is likely that temperatures somewhat below zero may also have a directly harmful effect on the eggs and the tiny larvæ. Experiments made by Prof. Aug. Krogh and myself[3]) in water of mean temperature — 1.7° and — 0.8° C showed that the eggs died before the embryo had developed, whereas the embryo developed in eggs kept in water at a constant temperature of 0° C. Temperatures of below 0° C. can, in cold winters, be observed down to a depth of several metres, and ice formation can take place at the lower surface of the upper, relatively fresh, water layer[4]). In the lower, salter bottom layer, the temperature does not fall

[1]) See Table 1 and Anton Fr. Bruun: Quantitative Investigations of the 0-Gr. and I-Gr. of the plaice etc. in the Skagerak, Kattegat and Belt Sea. — Medd. Komm. for Havundersøgelser. Serie Fiskeri, Bd. VIII, No. 5. København 1927.

[2]) J. P. Jacobsen and A. C. Johansen: Remarks on the changes in specific Gravity of pelagic Fish Eggs etc. Medd. Komm. for Havundersøgelser Ser. Fiskeri, Bd. III, Nr. 2, 1908.

[3]) A. C. Johansen and August Krogh: The influence of Temperature and certain other factors upon the rate of development of the Eggs of Fishes. Publications de Circonstance No. 68. Conseil perm. internat. Copenhague 1914.

[4]) C. I. H. Speerschneider: Om Isforholdene i danske Farvande i Aarene 1861—1906. København 1927.

below 0° C, and the eggs found there would thus undoubtedly be spared the harmful effect of the low temperatures.

It is probable, however, that both the low salinity and the low temperature exercise an indirect adverse influence on the numbers of young fry, namely, by reducing the available food supply. We know that the quantity of plankton in our waters is at its minimum in December, January and February, and this minimum is, in the Southern Kattegat and Belt Sea, even more pronounced than normally, when a strong outflow of relatively cold and less salt water from the Baltic takes place. Quantitative plankton investigations have shown that there is, on an average, less plankton per sq. metre of surface in the Baltic than in the

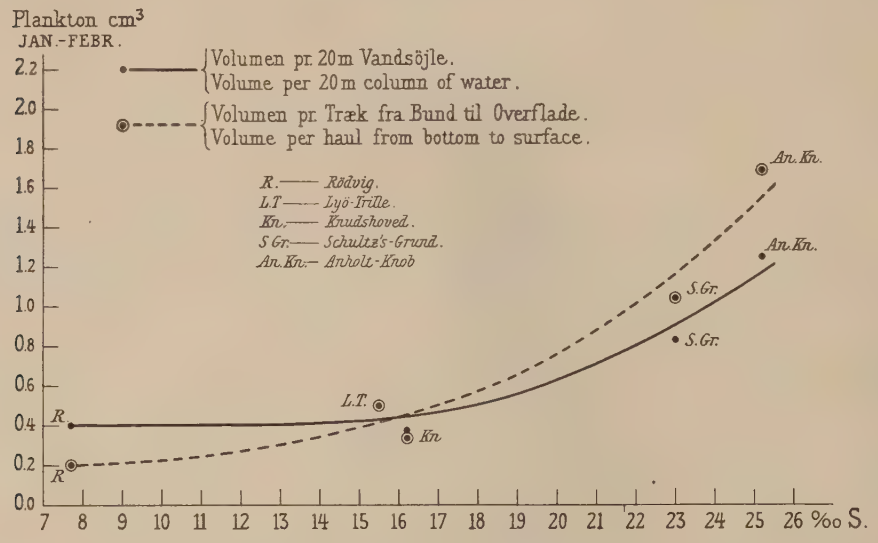


Fig. 5. Average volume of plankton collected by vertical hauls from bottom to surface during the months of January and February in water of different salinity (Stations: Rødvig, Knudshoved, Lyø Trille, Schultz's Grund, Anholt Knob).

Southern Kattegat and the Belt Sea, not only in winter, but also at other seasons of the year.

We find an indication of this already in the results of the plankton collections made, at the instigation of Dr. Petersen, from the Danish lightships and various other stations in 1898—1901 [1]). Fig. 5 shows the volumes of plankton taken by vertical hauls with a small plankton net with opening of 35 cm. diameter (No. 19 gauze), at various stations in the inner Danish waters, — viz. Rødvig, Lyø Trille, Knudshoved, Schultz's Grund and Anholt Knob, — compared with the mean salinity. The values noted for quantity of plankton are averages for 8 hauls taken in the months of January and February. One set of values denotes quantities of

[1]) C. G. Joh. Petersen: De danske Farvandes Plankton i Aarene 1898—1901. I. Kgl. D. Vid. Sel. Skr. mat. nat. Afd. vol. XII. København 1903.

plankton taken per haul from bottom to surface, the other indicates the quantity of plankton calculated per 20 metres' column of water. Both curves here give a

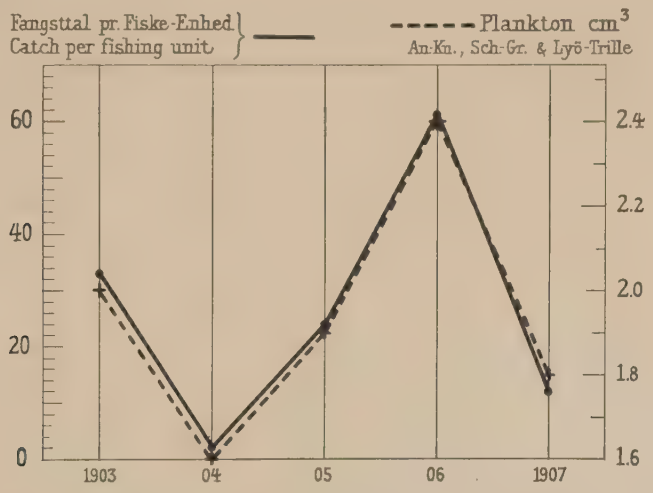


Fig. 6. Variation in the catch per fishing unit of plaice fry in the southern Kattegat and Belt Sea compared with the quantity of plankton at the Stations Lyø Trille, Schultz's Grund and Anholt Knob in January—February for the years 1903—1907. (At Schultz's Grund, no plankton collections were made in Jan.—Febr. 1907, but for this year the average value of the 4 preceding years is taken).

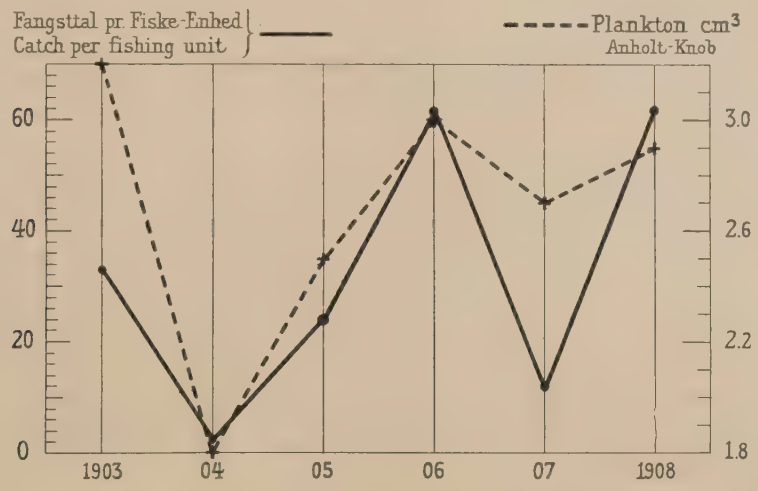


Fig. 7. Variation in the catch per fishing unit of plaice fry in the Southern Kattegat and Belt Sea compared with the quantity of plankton at Anholt Knob in January-February 1903—1908.

distinct impression of the marked increase in quantity of plankton from the Baltic through the Belts to the southern and middle Kattegat.

During the years 1903—06, vertical hauls were made from bottom to surface twice monthly with the above-mentioned little plankton net at the stations Lyø

Trille, Schultz's Grund and Anholt Knob. At Lyø Trille, the collection was continued in 1907 and at Anholt Knob in 1907 and 1908. A survey of the quantities of plankton collected has kindly been placed at my disposal by Professor C. H. Ostenfeld and Magister P. Jespersen. If we now compare the average quantity of plankton taken per haul in January and February with the figures for catch of young of the plaice, we find a close agreement for the few years during which investigations were carried out in both directions, as will be seen from Figs. 6 and 7. I would here point out that the catch figure for young of the plaice for 1903 is only approximately correct, as it is calculated from age analyses of older fish, not from actual catches of the 0-gr. and I-gr. fish on the coast. From a series of age analyses of grown up plaice from the years 1905—07 we can conclude that the year 1903 was, as regards the Southern Kattegat and Belt Sea, about a medium year for the quantity of young plaice.

The investigations made thus suggest that in cold winters, when there is a relatively marked outflow of comparatively fresh water from the Baltic through the Belts and the Southern Kattegat, the tiny plaice larvæ fail to obtain sufficient nourishment, and die of starvation *en masse.*

If future investigations should confirm the hypothesis that between the quantity of plankton and the number of young plaice there is a connection even approximately as close as Fig. 6 indicates, it will be possible to form a basis for estimating in advance the yield of the fishery more easily and cheaply by collecting plankton than from fishing experiments for young plaice. The quantitative plankton investigations should naturally be connected with researches as to what kind of plankton the tiny plaice larvae preferably feed on.

In conclusion, I would add a few remarks as to the possibility that the great fluctuations observed in the quantity of young may in some cases be due to the attacks of enemy species. This possibility cannot be disregarded. We know, for instance, in the case of the herring that the ova of this species which are found on the sea floor are keenly sought for by other species of fish, especially the haddock. It is also a well-known fact that the larvæ of cod, haddock, plaice, herring, and several other species are devoured *en masse* by Ctenophores, in our own waters more especially by Pleurobrachia pileus. Minor medusæ and various crustaceans also attack the pelagic fry. It is impossible, however, as yet to estimate the total effect of the extensive inroads made by these creatures on the young fry.

But, as the evidence to hand relative to the plaice in the Southern Kattegat and Belt Sea suggests that paucity of young fish in a given year is due to the presence of relatively fresh, cold water, deficient in plankton, during the winter months, which form the principal spawning season of this species, it is hardly likely that the attack of numerous enemies should here be the direct cause of the smaller quantity of young.

II.

On a Spawning Place for winter spawning Herring in the northern part of the Belt Sea.

By

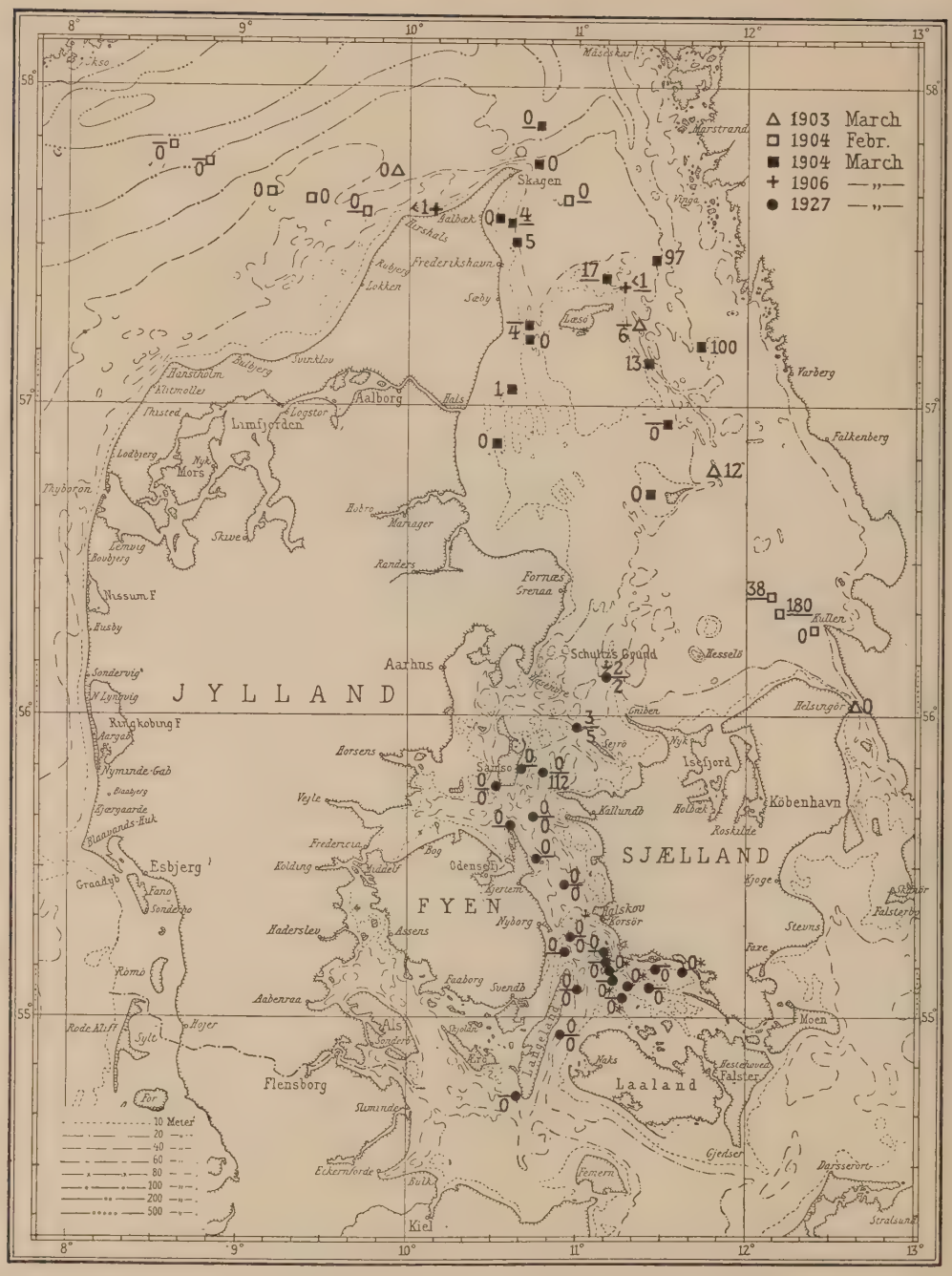
A. C. JOHANSEN.

In the eastern and south-eastern Kattegat there occurs, as I have previously shown[1]) a special group of herring, whose main spawning season falls in the middle of winter, i. e. in January and February. By fishing experiments, with a large stramin net mounted as a "Young-Fish-Trawl" with otter boards or as a "Ring-Trawl", carried out from the Research Vessel "Dana" for several years in April and May, larvae of winter spawning herring have been caught in considerable numbers, but since numerous pelagic organisms are carried along with the undercurrent from the eastern Kattegat to the Belt Sea it was uncertain whether these larvae originated from the winter spawning herring in the eastern Kattegat or from winter spawning herring which spawned in the Belt Sea itself. In order to throw light on this question, a series of fishing experiments with ring-trawl[2]) were carried out in the Belt Sea at the beginning of March 1927 from the Biological Station's Steamer „Japetus Steenstrup" and as may be seen from the map Fig. 1 a considerable number of quite recently hatched herring larvae, from 7 to 9 mm. in length, were caught between Schultz's Grund and East of Samsø, several of them possessing yolk sacs. It was quite obvious that these recently hatched larvae could not have originated from the eastern Kattegat since many of them were scarcely one week old, and transport with the undercurrent from the eastern Kattegat to Schultz's Grund takes generally about one month. In addition to this is to be reckoned the fact that the greatest number of larvae were not caught in the most northern part of the Belt Sea but in the channel East of Samsø, and that the mean size of the larvae was less there than in the other parts of the Belt Sea.

---

[1]) A. C. Johansen. "Ueber die Winterheringe des Kattegats" Wiss. Meeresuntersuch. N. F. Abt. Helgoland. XV. Bd. Festschrift für Heincke. Oldenburg. 1923.

[2]) The mouth of the ring-trawl was approximately 2 metres in diameter and thus had an area of about 3 square metres. In some cases a young-fish-trawl with a mouth 2 square metres in area was employed. In the calculation of the haul per unit of time the number of larvae caught with the young-fish-trawl is multiplied by 1.5 to enable a comparison to be drawn with the number caught with the ring-trawl.


1903 March
1904 Febr.
1904 March
1906 —„—
1927 —„—
JYLLAND
FYEN
SJÆLLAND
Laaland
Skagen
Aalborg
Aarhus
Esbjerg
Flensborg
Kiel
København
Schultz's Grund
Frederikshavn
Frederica
Nyborg
Odense
Korsør
Roskilde
Helsingör
Falkenberg
Varberg
Marstrand
Lemfjorden
Limfjorden
Nissum F.
Ringkobing F.
Thyboron
Hanstholm
Skive
Randers
Fornæs
Grenaa
Hesselø
Kullen
Lesø
Anholt
Læsø
Skagerak
Kattegat
Sylt
Rømø
Fanø
Als
Alsen
Fehmern
Gjedser
Darsserort
Stralsund
Meen
Falster
Stevns
Faxe
Kjoge
Ise fjord
Holbæk
Kallundb
Svendb
Assens
Haderslev
Aabenraa
Kolding
Veyle
Horsens
Samsø
Seyrø
Gniben
Ebeltoft
Grenaa
Hals
Løgstør
Thisted
Lodbjerg
Mors
Bovbjerg
Lemvig
Hvide Sande
Ringkobing
Nymindegab
Blaavands-Huk
Grindsø
Rødekro
Tønder
Ribe
Varde
Vejle
Middelf
Bog
Tjerem
Hjelskov
Ballebro
Fredericia
Helnæs
Ærø
Langeland
Taasinge
Bagenkop
Rudkøbing
Svendborg
Nyborg
Korsør
Kalundborg
Holbæk
Roskilde
Køge
Stevns
Faxe
Falsterbo
Moen
Gjedser
Darsserort
Stralsund
Kiel
Eckernförde
Flensburg
Apenrade
Hadersleben
Esbjerg
Ringkøbing
Nymindegab
Blaavandshuk
Hvide Sande
Lemvig
Bovbjerg
Thyborøn
Hanstholm
Klitmøller
Thisted
Løgstør
Lodbjerg
Mors
Nissum F.
Ringkøbing F.
Skive
Randers
Grenaa
Hesselø
Kullen
Helsingör
Falkenberg
Varberg
Marstrand
Skagen
Frederikshavn
Aalborg
Limfjorden
Aarhus
Schultz's Grund
København
Roskilde
Holbæk
Kallundb
Ise fjord

As may be seen from Fig. 2, the mean size of the larvae increases the further one goes from Samsø Belt both in a northerly and in a southerly direction.

As is known, the herring deposits its eggs on the sea bottom and the precise situation of the spawning places cannot be fixed by catching the tiny herring larvae with ring-trawl or young-fish-trawl. One can however by fishing experiments with these implements point out roughly within which regions spawning takes place. As may be seen in Fig. 2, larvae of winter spawning herring were found in March 1927 both in Store Belt and Langelands Belt, and in the Smaaland Sea, but none of the recently hatched larvae with yolk sacs were caught here. There is every reason to suppose that the larger larvae of winter spawning herring which were caught there had been transported thither from the northern part of the Belt Sea.

The lengths of the larvae of winter spawning herring caught in the Belt Sea between the 1st and the 10th of March 1927 were as follows:

Length in millimetres.	Number of larvae.
7	2
8	33
9	89
10	70
11	47
12	60
13	49
14	35
15	21
16	14
17	3
	Total 423

Average length in millimetres 11.2

The average length of all the larvae of winter spawning herring, which were caught in the Belt Sea between the 1st and the 10th of March 1927, was thus approximately 11 mm. Upon being hatched the larvae of the winter spawning herring have a length of about 5—6 mm. and, according to data collected concerning the growth of herring larvae in winter, the average age of the larvae caught may be estimated at approximately 1 month. Since the temperature of the water in the Belt Sea in January and February is known, as is also the length of the hatching period of the eggs at various temperatures, it is possible to calculate approximately when the main spawning has taken place. The mean temperatures of the lower water layers at Schultz's Grund and at Halskov Rev in January and February 1927 were as follows:[1])

[1]) Nautisk-Meteorologisk Aarbog. København 1927.

Fig. 2. Number of larvae of winter spawning herring caught per 30 mins. haul with stramin ring-trawl from the 1st to the 10th of March 1927. The figures in parenthesis indicate the average length of the specimens in millimetres, as calculated by Erik M. Poulsen. (See also explanation to Fig. 1).

	Schultz's Grund		Halskov Rev
	20 m	26 m	20 m
January	4.3° C	5.7° C	3.8° C
February	4.6° C	5.0° C	4.0° C

The mean temperature of the bottom water in the northern part of the Belt Sea in January and February has thus been from 4° C. to 6° C. approximately.

At a temperature of 5° C. the hatching of herring eggs takes about 25 days, and the main spawning must thus have taken place about the middle of January. A number of the largest larvae of the winter spawning herring probably originate from eggs deposited already in December, whilst the smallest larvae obviously originate from eggs deposited in February.

It will be seen, on consulting the table showing the distribution of the larvae according to their length, that their number reaches a maximum at 9 mm. and another maximum at 12 mm. This second maximum is due probably to the circumstance that there has been more fishing for large larvae in the middle regions of the Belt Sea than for small larvae in the northern regions.

In the spring months there is a distinct difference in size between the larvae of the winter spawning herring and those of the autumn spawning herring. Whereas the larvae of the winter spawning herring had a mean length of 11 mm. at the beginning of March 1927, the larvae of the autumn spawning herring had a mean length of 25—30 mm. The autumn spawning herring in the Belt Sea have their main spawning season in September and October.

There is also a distinct difference in size between the larvae of the spring spawning herring and those of the winter spawning herring in the Belt Sea, which fact has been observed several times by fishing experiments from the Research Vessel "Dana". In the days round about the 1st of June 1923 the larvae of the spring spawning herring in the Belt Sea had a length of 5 – 15 mm. with a mean length of about 10 mm., while the larvae of the winter spawning herring were 18—31 mm. in length and had a mean length of about 25 mm. The difference in size corresponds to a difference in the time of spawning of about 3 months. Whereas the winter herring in the Belt Sea spawn in January and February, the main spawning season of the spring herring is in April and May. The spring herring begin to spawn in March or April and do not cease until the beginning or middle of June.

While the experiments carried out have proved the existence of a spawning place for winter spawning herring in the northern part of the Belt Sea, the actual racial characteristics of this race of herring are not yet known with any degree of certainty, since specimens of it have not been examined when fully ripe (with running roe or milt). A young herring from the northern part of the Belt Sea is however known which has the same or very nearly the same racial characteristics as the herring which spawns in the winter months in the south-eastern Kattegat, so it may fairly safely be assumed that this young herring

belongs to the race of winter herring which spawns in the Belt Sea. It possesses a greater number of vertebrae than the spring and autumn herring which spawn in the Belt Sea[1]).

Very little is yet known as regards the importance of the winter spawning herring for the fishery in the Belt Sea. It is not fished for in the spawning season and thereby, in contrast to both the spring and the autumn spawning herring, it escapes capture by fishermen to any appreciable extent. The stock of winter spawning herring in the Belt Sea is probably much smaller than the stock of either the spring spawning or the autumn spawning herring. This is indicated by the fact that the pelagic larvae of the winter herring are caught by fishing experiments with young-fish-trawl and ring-trawl in considerably less numbers than are the larvae of spring and autumn herring. But the fact that there are great fluctuations in the size of stocks within periods of some few years' duration applies to all races of herring.

---

[1]) Several races of spring spawning herring and at least two races of autumn spawning herring are found in the Belt Sea. A feature common to all the autumn spawning herring in the waters of the Baltic is that they have a relatively greater number of precaudal vertebrae than have the spring spawning herring.

II.

On the Annual Fluctuations in the Age-composition of the Stock of Plaice.

Investigations from the Danish Biological Station 1923—26.

By

H. BLEGVAD.

CONTENTS

Page

Introduction 27

I. *The Belt Sea and Southern Kattegat.*

A. Taken in fine-meshed otter seine („Eel-Tog") 29

B. Purchased from Fishermen, taken in otter seines, stake nets and Danish seines 33

C. Yield of the plaice fishery 35

II. *The Sound.*

A. Taken in Eel-Tog 37

B. Purchased from Fishermen 38

III. *Northern Kattegat.*

A. Taken in Eel-Tog 38

B. Purchased from Fishermen. Taken in Danish seine 39

IV. *The Limfjord.*

A. The Nissum Broad. All taken in Eel-Tog 39

B. The Inner Broads of the Limfjord. All taken in Eel-Tog 40

INTRODUCTION

For some years past, fishing experiments have been carried out in Danish waters inside the Skaw from the Danish Biological Station's vessel „Japetus Steenstrup". The plaice taken in the course of these experiments were classified as to age immediately after capture by the present writer, the work being carried out on board, so that it was possible at once to ascertain the age composition of the sample in question. In the course of this work, it has often struck me as remarkable that when we found the II-Group for instance, in one year predominating over all other age-classes in a given locality, the following year would often show the I- or III-Group as most numerous. The material from the last three years especially has exhibited this feature to a remarkable degree; a fact which naturally suggests the alternation of favourable and unfavourable years for the young plaice. Whether this is the true explanation however, is another question, and I have therefore taken up the whole of the material for closer investigation. I must first of all however, make some observations as to the nature of the material.

The different age-classes of plaice often keep, as we know, to different depths, and care has therefore been taken to fish in so many different places that we could be sure of getting a fairly representative sample of the stock in the water in question. I have however, been obliged to disregard the 0-Group almost entirely, as these fish keep as a rule to such shallow water that special implements are required for their capture, and quantitative comparison of the 0-Group with the remaining age-classes is thus a very difficult matter. The remaining age-classes were taken mostly with the „Eel-Tog", an almost rectangular otter seine without arms, abt. $3^1/_2$ m wide, 9 m long and 0,9 m high at the mouth. The meshes nearest the mouth are 18 mm from knot to knot, at the hinder end 15 mm. The „Eel-Tog" was used as a rule with 20 m lines between net and otter boards, sometimes however, with lines of 100 metres' length. It is handy to use, and has proved extremely suitable for the capture of flatfishes, both large

and small. Experiments have shown that it will take plaice right down to 4 cm long and it is therefore possible to take plaice of the 0-Group with this implement in deeper water, especially in the autumn; and as we shall see later on, this fishery also affords valuable information concerning the 0-Group. Finally, it is very useful for the purpose of comparative quantitative fishery.

In order to supplement the catches made with this finemeshed implement, samples have occasionally been purchased from the fishermen's hauls, especially with a view to ascertaining which of the age-classes formed the principal basis of the fishery.

With regard to the distribution of the age-classes in the Baltic proper, I have already, in Report XXXII from the Danish Biological Station 1926 („On the Renewal of the Stock of Plaice in the Baltic proper") p. 24, stated that the investigations of the Danish Biological Station in 1925 and previous years showed the year-classes 1925, 1923, 1921 and 1919 as comparatively richly represented in the Baltic proper, whereas year-class 1924 was almost entirely lacking, and 1922 but very poorly represented. Fishing experiments in the Baltic proper during 1926 have fully confirmed this result, the distribution of year-classes in a batch of 392 plaice being as follows:

Year-class 1926: 14 specimens (3,6 %), 1925: 143 (36,4 %) 1924: 1 (0,3 %), 1923: 78 (19,9 %). 1922: 36 (9,2 %) 1921: 59 (15 %) 1920 and older: 61 specimens (15,6 %). The rich year-classes are underlined.

The hand push net accounted for 60 specimens of the 0-Group in 1926, these being taken at 10 different localities on the shores of the Baltic proper, 6 specimens being from Bornholm. This rather suggest that 1926 must have been a medium year for the young plaice in the Baltic proper.

I. The Belt Sea and Southern Kattegat.

A. Taken in Eel-Tog.

On going through the extensive material from our fishing experiments and age determinations it was found that the general features were fairly uniform as regards the age-composition of the stock within the area Great Belt — Lesser Belt — Samsø Belt — Isefjord — Southern Kattegat (the waters south of Hals-Anholt). I have therefore worked out the results for this area as a whole, and obtained the following values:[1])

Southern Kattegat and Belt Sea.

Taken in Eel-Tog.

No. of Plaice in	0-Group	I-Group	II-Group	III-Group	IV-Group	V-Group	Older	Total
1923:	35	57	294	65	19	3	»	473
1924:	1	320	55	89	6	1	»	472
1925:	28	45	486	15	6	»	»	580
1926:	22	709	157	346	4	»	1	1239
			Expressed in %:					
1923:	7,4	13,2	62,1	13,7	4,0	0,6	»	
1924:	0,2	67,8	11,6	18,9	1,3	0,2	»	
1925:	4,8	7,8	83,8	2,6	1,0	»	»	
1926:	1,8	57,2	12,7	27,9	0,3	»	0,1	

Fig. 1 gives a graphical illustration of the position. It will be noticed that in 1923 and 1925, the II-Group was more numerous than any of the others,

[1]) I have omitted a few specimens which could not be classified as to age, and some where the determination was doubtful. The number of these rejected specimens is, however, so very small — less than 2 % of the entire material divided among the different age classes — that the omission may be taken as insignificant.

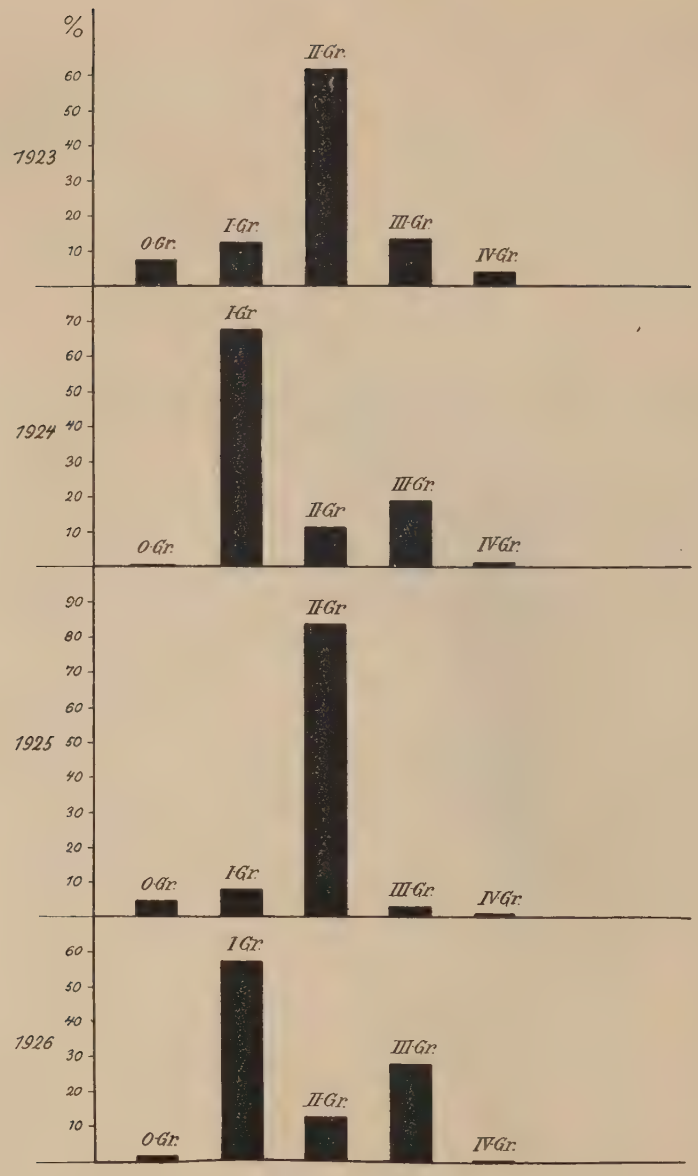


Fig. 1. Distribution, in percentage, of the Age-classes in the Belt Sea and Southern Kattegat during the years 1923—26. Eel-Tog.

whereas in 1924 and 1926, it was the I-Group and the III-Group which predominated. Plaice of 5 years and over were taken in such small numbers that we may disregard them altogether, and they have therefore not been reckoned with in the graph; it should also be borne in mind that the numerical value of the 0-Group cannot be seen from Fig. 1, as this group is, for the greater part of the summer, found only in quite shallow water, where the Eel-Tog cannot be used. It would seem, however, from the relatively considerable numbers of 0-Group plaice taken with the Eel-Tog in the autumn of 1923 and 1925, that these were particularly good fry-years (i. e. years in which particularly many individuals reached the bottom stage), whereas 1924 must evidently have been a very bad fry-year (i. e. a year in which particularly few individuals reach the bottom stage); which, as we shall see later on, is fully borne out by the remaining facts.

That the material is really representative, i. e. gives a reliable view of the age composition of the stock of plaice (apart from the 0-Group) is apparent from the following:

1) The implement used is equally well suited to the capture of large and small plaice, as has been proved by comparative fishing experiments with smaller- and larger-meshed nets.

2) So many hauls were made, at so many localities, that the figures given must be presumed to afford a good picture of the composition of the stock of plaice for the four years in question. The investigations were carried out each year from the beginning of April to some way on in October. In 1923, fishing experiments were made at 44 different places in the Belt Sea and Southern Kattegat, in 1924 at 31 different places, in 1925 at 32, and in 1926 at 68 localities.

3) There is close agreement between the age-groups from one year to another. The dominant II-Group of 1923 for instance, appears again in 1924 as a fairly numerous III-Group, The large I-Group of 1924 has in 1925 become an enormous II-Group, and in 1926 is still dominant to some extent as the III-Group etc. etc.

Now what are we to conclude from these fluctuations in the age-composition of the stock of plaice? Dr. A. C. Johansen has already shown (Contrib. to the Biology of the Plaice III. Medd. Komm. f. Havunders. Serie Fiskeri Vol. III No. 4, 1908 p. 20) that when the 0-Group was very poorly represented in any given year (as here in 1904), the fact could be traced in the catches of the years immediately following (here 1905—1907), this year-class proving throughout less numerous than the preceding and the two succeeding year-classes. He further points out that this shortage of 0-Group plaice in 1904 is most probably due to an unusually low salinity of the surface water in the Kattegat, and to some extent also in the Belt Sea, during January to March 1904.

In my own earlier work above mentioned, on the stock of plaice in the Baltic (Rep. Dan. Biol. St. XXXII 1926) I have shown that similar conditions have during recent years prevailed in the Baltic, where low temperature and low salinity in the lower water layers during Jan.-April 1924 are doubtless correlated with the fact that 1924 proved a remarkably poor fry-year for the plaice in the Baltic proper. The year 1925 on the other hand, which was a particularly good fry-year for the plaice of the Baltic proper, was one of high temperature and salinity during the first months of the year; this was also the case in 1923 and 1921, and I therefore consider the comparatively high percentage of these year-classes in the catches of 1924 and 1925 as due to the fact that 1925, 23 and 21 were god fry-years. The year 1922 on the other hand was, like 1924, a poor fry-year for the plaice in the Baltic proper, with ice and low salinity recorded in the first months of the year.

The distribution of the age-classes among the stock of plaice in the Belt Sea and Southern Kattegat in 1923—26 (Fig. 1) likewise admits of but one explanation; that we have here good and bad fry-years alternating. For if there had been the same numbers of fry growing up each year, then we should, in Fig. 1, find the I-Group most numerously represented throughout, followed by the II-

Group, the III-Group and so on; for the rate of death increases with age, more especially owing to the effect of the fishery, which is chiefly directed towards the older fish.

When then, we find, in 1923, not the I-Group but the II-Group as the most numerously represented age-group, we can only interpret this as meaning that the I-Group (the 1922 year-class) must be the product of a poor fry-year, the II-Group (year-class 1921) of a comparatively good one.

Similarly, the distribution of the age-groups in 1924 confirms the suggestion that 1922 was really a comparatively poor fry-year for the plaice, and 1921 a good one, since we have here the III-Group more numerously represented than the II-Group. The large I-Group suggests that 1923 was a good fry-year, and the fact than only a single plaice of the 0-Group was taken in all the numerous fishing experiments made that autumn suggests that 1924 must have been an uncommonly bad year for the production of yong plaice in these waters.

This is again confirmed by the results for 1925, where the I-Group (the 1924 year-class) was particularly poorly represented, but the 1923 year-class (the II-Group) was numerous. The not inconsiderable numbers of 0-Group plaice taken in deep water during the autumn rather suggests that 1925 was a good fry-year.

This is confirmed by the fishing experiments in 1926, the results of which say: good production in 1925, bad in 1924, good again in 1923. The relatively poor 0-Group here rather suggests that 1926 was somewhat below the average, but this we cannot say for certain until the results of the 1927 investigations are available.

It might perhaps here be objected that it is impossible to determine, from the material here in question, whether a given age-group really was more numerous in one year than in another, in that our figures are all relative and therefore say nothing as to the density of the stock or the year-classes per unit of area. We can however, form an idea as to this by considering the amount of time occupied in capturing the number of specimens recorded during the different years, the implements used being the same throughout. The I-Group is the one likely to give the most reliable view of the density of the year-classes throughout a period of years, as it is relatively unaffected by the fishery; I therefore give below the numbers of specimens of this age-group caught per hour in the different years. The figures are as follows:

In 1923,	57	specimens	of the	I-Group	in	1251 min.	or 2.7	specimens per hour.
» 1924	320	»		»		815 min.	or 23.6	» per hour.
» 1925	45	»		»		825 min.	or 3.3	» per hour.
» 1926	709	»		»		1754 min.	or 24.3	» per hour.

It will be seen that these figures entirely confirm the correctness of the

conclusions drawn in the foregoing from the values in Fig. 1. Furthermore, the figures here given, always provided that they are sufficiently representative, show also that the I-Group in 1924 and 1926 was of about the same size, and amounted to something like eight times the stock of the I-Group in 1923 and 1925. Assuming further that the wastage percentage in course of growth from 0-Group to I-Group has been uniform in all years, this means that as regards the production of young plaice in the Belt Sea and Southern Kattegat, the years 1923 and 1925 were eight times as good as 1922 and 1924.

As regards the older age-groups, (IV-Group and V-Group etc.) no conclusions can be drawn from the material available, as the intensive fishery carried on in these waters steadily keeps down the numbers of older plaice to a merely minimal figure, whether they derive from a rich year-class or a poor one.

We find then, that the fishing experiments for all four years exhibit a nice agreement in their results, indicating also, that we have a regular alternation of good and bad fry-years from 1921 to 1926, the »odd«years 1921, 23 and 25 being good fry-years, the »evens«, 1922 and 1924 on the other hand being bad in this respect. Our results here then, are in entire agreement also with those noted in the foregoing for the Baltic proper.

Also as regards the causes of these fluctuations between good and bad fry-years we find, on going through the temperature and salinity records from lightships in the Southern Kattegat and Belt Sea (Nautical Meteorological Year-book 1921—25) that during the spawning time of the plaice — the four first months of the year — comparatively high temperatures and salinities prevailed at nearly all depths in these waters during the rich fry-years 1921, 1923 and 1925, whereas the bad years 1922 and 1924 opened with severe ice winters and long periods of very low salinity. With regard to the marked inflow of salt and warm North Sea and Atlantic water into the Kattegat and the Belt Sea in the early part of 1923, the reader may refer to A. C. Johansen: On the Influence of the Currents upon the Frequency of the Mackerel in the Kattegat and adjacent parts of the Skagerak«. Medd. Komm. f. Havunders. Serie Fiskeri. Vol. VII Nr. 8 1925.

B. Purchased from Fishermen. Taken in otter seines, stake nets and Danish seines.

In 1924 and 1925, only a very few plaice were purchased from the fishermen; in 1923 on the other hand, 186 specimens were bought and examined, and 315 in 1926.

The age-investigation gave the following result:

	I-Group	II-Group	III-Group	IV-Group	V-Group	Older	Total
1923:	»	43	83	24	14	22	186 Spec.
(7 Localities)							
1926:	39	105	152	10	2	7	315 »
(11 Localities)							
Expressed in %:							
1923:	»	23,2	44,6	12,9	7,5	11,8	
1926:	12,4	33,3	48,3	3,2	0,6	2,2	

From a comparison of this table with that at page 29 it will at once be seen that the catches made by the fishermen do not afford any representative view of the stock, but only a selected sample of the same. The great majority of the I-Group for instance, escape capture by the fishermen, being for the most part small enough to pass through the meshes of their nets. The fact that we found no I-Group plaice at all among the fishermen's catch in 1923 agrees with the ascertained paucity of this group in that year. The 39 specimens of the I-Group from 1926 are partly from the Bay of Aalborg, partly from the Lesser Belt, and all were taken during autumn. In the spring, practically all the I-Group plaice pass through the fishermen's nets, or have to be returned, if caught at all, as undersized. It is interesting to note that the great majority of the fishermen's catch, both in 1923 and 1926, when conditions generally were otherwise highly dissimilar (see Fig. 1) consisted of III-Group fish, though a very essential portion was made up of II-Group specimens, and this despite the fact that the II-Group in 1926 originated from a bad fry-year and was thus but poorly represented in proportion. This explains why there are never very many IV-Group plaice in these waters, and that the III-Group in the year following one with a naturally poor II-Group, will be further impoverished, as for instance the III-Group in 1925 (see Fig. 1); the same will undoubtedly be the lot of the III-Group in 1927.

The above-noted samples of the fishermen's hauls are all from the summer half-year, save for a single sample from the Great Belt (Deep channel, off Kerteminde) taken in the winter of 1923/24. In this sample, the IV- and V-Group fish are more numerous than both the II-Group and the III-Group, showing that the older plaice assemble in the deep channels during the winter half-year for spawning.

In the waters between Funen and Langeland, which form a particular haunt of the young plaice, and where no plaice fishery of any importance is carried on during winter, the fishing experiments made with the Eel-Tog during 1926 give a typical instance of the marked influence of the fishery on the age-composition of the stock. The age-groups were represented as follows:

	I-Group	II-Group	III-Group	Total investigated
10'—11' May 1926:	14%	7%	79%	29 Specimens
16'—17' June 1926:	22%	18%	60%	238 »
13'—14' Sept. 1926:	71%	23%	6%	31 »

In spring then, the III-Group was most numerous, but by June, the number had already considerably decreased, and in the autumn, the III-Group was almost fished out; the fishery had by now almost come to an end, as it was no longer worth while. Even though the marked increase in the numbers of the I-Group may possibly be due to immigration of young plaice from the shallow water along the coast, there can be no doubt that the principal cause of the disappearance of the III-Group is the intensive fishery with otter seine and stake net in these waters.

Something similar is found to be the case in the Smaaland waters (S. of Sealand), where our fishery with Eel-Tog in 1923 gave the following results:

	0-Group	I-Group	II-Group	III-Group	IV-Group	Total investigated
29' May 1923:		4%	11%	58%	27%	26 Specimens
7' Aug. 1923:	4%	10%	55%	30%	1%	112 »

According to this, the II-Group and IV-Group were, in the course of a good two months, reduced from 58% and 27% respectively of the stock to 30% and 1% respectively. Even though our figures here are too low to warrant definite conclusions, they may undoubtedly be taken as affording an approximately correct view of the position.

It is not surprising therefore that nearly half the fishermen's catch consists of plaice between 3 and 4 years old and $^1/_3$—$^1/_4$ of those between 2 and 3 years old (see page 34). Not even the I-Group is completely protected by the present size-limit of 25.7 cm, since, as we have seen, 12% of the fishermen's catch in 1926 consisted of $1^1/_2$ year old fish. That plaice should be taken at such an early age, when they are far from having attained an adequate weight and value, is a serious reminder of the necessity for having the size-limit raised as soon as possible for these waters.

C. Yield of the Plaice Fishery.

Which distribution of the age-groups is more advantageous to the fishery: 1) to have a large II-Group to draw upon, as in 1923 and 1925, or 2) to have a dominant I- and III-Group as in 1924 and 1926?

According to the »Fiskeri-Beretning« for the years 1923—25, the yield of the plaice fishery during those years was as follows:

	Belt Sea	Kattegat
1923:	1.363.151 kg	1.664.699 kg
1924:	1.028.167 »	1.454.706 »
1925:	1.030.269 »	2.000.731 »

1923 and 1925 were thus the best years in both waters. This might seem to suggest that a large II-Group gives the better yield, but the difference here, especially as regards the Belt Sea, is so slight that one can hardly draw any conclusions from this. It should also be borne in mind that the greater part of

Fig. 2. Yield of the Plaice Fishery from Kongshøjaa to North of Thurø in 1923–26.

the II-Group are, during the first half of the year, still undersized (i. e. below 25.7 cm) and therefore must not be taken. According to measurements from the Biological Station, only abt 8 % of the II-Group in the Belt Sea during May and June have reached the size limit for capture; not until August do we find nearly half (46 %) have attained this size. In the Southern Kattegat, in July, 41 % of the II-Group were of retainable size. The III-Group on the other hand, in the Belt Sea, has 36 % in May, 43 % in June, 72 % in July and 83 % in August. One would therefore suppose that the fishery at the beginning of the years when the stock consists mainly of II-Group fish would be poor, and that of the autumn good. Something of this sort is also indicated in the monthly records of the Fishery Statistics, which I have been able to consult, thanks to the courtesy of the Board of Fisheries; the picture is however, often obscured, partly because the

fishery at the beginning of the year is based more particularly on the older fish (IV-Group and over) still left over from the preceding year, which assemble in the deeper channels during winter; partly, again, because it is impossible as a rule to obtain exact data as to number of fishing days or fishing grounds; and finally also because ice or other conditions may affect the yield.

By way of example, I give in Fig. 2 the curves for yield of the plaice fishery along the range from Kongshøjaa to north of Thurø; I have chosen this locality because the fishermen there work predominantly in the »Fresh Water« i. e. the waters between Funen and Langeland, where the stock consists almost exclusively of fish under 4 years old.

From this it will be seen that, apart from 1924, which opened with a severe ice winter, the yield in 1923 and 1925 was relatively slight during the first months of the year, whereas in the last months of the year it was considerably better than both 1924 and 1926. Had the yield been stated in no. af specimens in stead of in kilos, the difference would doubtless have been even more clearly apparent.

As regards the prospects for the fishery in 1927, there can be little doubt but that the II-Group will be the dominant age-class, the III-Group being relatively poor in numbers. We may therefore expect that the spring fishery will be poor, the autumn fishery on the other hand, especially in places where the II-Group has its main occurrence, e. g. in the Bay of Aalborg, the Smaaland waters, in the Lesser Belt and the »Fresh Water« considerably better.

II. The Sound.

A. Taken in Eel-Tog.

	I-Group	II-Group	III-Group	IV-Group	V-Group	Older	Total investigated
No. of plaice in 1923:	1	4	56	17	29	8	115 specimens
» » » » 1924:	»	»	31	85	14	10	140 »

In 1925 and 1926, the numbers of specimens taken were too small to warrant any definite conclusions from the figures. It will be seen from the values quoted above for 1923 and 1924 that the stock of plaice in the Sound, where seine fishing is forbidden, consists of much older fish than in the Belt Sea and Southern Kattegat; the figures therefore give no information as to the younger year-classes. The III-Group in 1923 and the IV-Group in 1924 — i. e. the 1920 year-class — were particularly numerous. The distribution of the age-classes very much resembles that found in the Baltic in Køge Bay and at Stevns (see Rep. Dan. Biol. St. XXXII, p. 23, the figures for 1924); this in conjunction with several other features, suggests that the plaice of the Sound are largely derived

from the Baltic. Altogether, the Sound must doubtless be regarded as a »migration locality« for the plaice; the I-Group and II-Group never seem to be present here in any great numbers.

B. Purchased from Fishermen.

On the $^2/_7$ 1924 a catch of 33 plaice was purchased from the stake nets off Snekkersten; the distribution was as follows: II-Group 7 specimens, III-Group 4, IV-Group 11, V-Group 11 specimens. The two oldest age-groups were thus the most numerous; the total number however, is too small to warrant further conclusions as to the distribution of year-classes here.

III. Northern Kattegat.

A. Taken in Eel-Tog.

	I-Group	II-Group	III-Group	IV-Group	Total investigated
No. of plaice in 1923:	104	64	6	»	174 specimens
» » » » 1924:	58	55	9	»	122 »
» » » » 1925:	85	160	19	»	264 »
» » » » 1926:	481	121	11	3	616 »
Expressed in %:					
1923:	59,8	36,8	3,4	»	
1924:	47,5	45,1	7,4	»	
1925:	32,2	60,6	7,2	»	
1926:	78,1	19,6	1,8	0,5	

The bulk of the catches here noted are from the Bay of Aalbæk and the waters round Læsø Rende and by Hals.

There are, as will be seen, no great alternations here in the age-composition of the stock from year to year. The I-Group is as a rule the most numerous, then come the II-Group, the III-Group and so on. The 1924 year-class however, seems, as in the Southern Kattegat, to have been a poor one, though not by any means so poor as in the more southerly waters; 1925 is the only year in which the I-Group is less numerous than the II-Group. Again, in 1926, the II-Group was relatively poor in numbers, amounting only to 19,6% of the whole. This last may, however, be partly due to the fact that the 1925 year-class was unusually rich; from the present material we can only see that the year-classes 1922, 1923 and 1925 were all richly represented, 1924 on the other hand being poor in comparison with 1923 and 1925. On the whole, there seems to be a fair abundance of young plaice in these waters every year, which accords well with the fact that ice winters are very rare here, and the salinity never falls so low as to be likely to approach the fatal minimum for plaice eggs or larvæ.

B. Purchased from Fishermen. Taken in Danish Seine.

Some few samples from the fishermen's hauls in the Bay of Aalbæk and on the Læsø Rende grounds were purchased in 1923 and 1926. Age analyses gave the following result:

		II-Group	III-Group	IV-Group	Total investigated
25—28/VI 1923	(3 localities)	31	39	2	72 specimens
1—2/VII 1926	(2 »)	28	27	1	56 »

The material is not sufficient in itself to warrant any sort of conclusions; I think however, that it gives a correct view of the fishermen's catches on the shallower grounds. The large numbers of I-Group plaice found here will doubtless nearly all pass through the mesh of the nets used. The fact that the fishermen take nearly as many plaice of the III-Group as of the II-Group, though the latter is far more numerous than the former, shows that a very high proportion of the II-Group also pass through the meshes of the nets.

IV. The Limfjord.

A. The Nissum Broad. All taken in Eel-Tog.

	0-Group	I-Group	II-Group	III-Group	IV-Group	V-Group	VI-Group	Total investigated
No. of plaice in 1923:	»	2	23	49	33	12	2	121
» » » » 1924:	»	5	45	16	49	17	»	132
» » » » 1925:	34	16	80	75	14	7	1	227
» » » » 1926:	33	1030	131	110	38	5	»	1347
Expressed in %:								
1923:	»	1,7	19,0	40,5	27,2	9,9	1,7	
1924:	»	3,8	34,1	12,1	37,1	12,9	»	
1925:	15,0	7,0	35,3	33,0	6,2	3,1	0,4	
1926:	2,4	76,5	9,7	8,2	2,8	0,4	»	

Compared with the Kattegat and the Belt Sea, the stock of plaice in this over-populated water consists of rather old fish. Particularly noteworthy is the relatively high figure for the III-Group in 1923, and, correspondingly, for the IV-Group in 1924. This suggests that the 1920 year-class must have been an unusually rich one in the adjacent areas of the North Sea, from which the Limfjord plaice must presumably be derived; for as we know, the plaice do not spawn in the Limfjord itself. The 1921 year-class on the other hand seems to have been comparatively poor. The samples from 1924 and 1925 show that both 1922 and 1923 were fairly rich years, the II-Group being numerous both in 1924 and 1925,

the III-Group similarly in 1925. The 1924 year-class on the other hand seems to have been a poor one. Particularly noticeable is the enormously high figure for the I-Group in 1926, this group being absolutely predominant over all the rest, though the I-Group in other years is more or less insignificant. This can only be explained by supposing that a huge invasion of plaice of the 1925 year-class must have taken place, the fish moving in to Nissum broad from the North Sea, where this year-class must have been particularly rich*). We can see from the available material that this invasion commenced in the summer of 1925, but did not proceed on an extensive scale until the summer of 1926, the distribution according to year-classes being as follows:

Year-class:	1926	1925	1924	1923	1922	1921	1920	1919	Total
Taken in May 1925:	»	»	7	44	40	10	5	1	107 specimens
» » Sept. » :	»	34	9	36	35	4	2	»	120 »
» » April 1926:	»	33	17	44	20	4	»	»	118 »
» » Sept. » :	33	960	82	46	7	1	»	»	1129 »

It will be seen that though there are already a number of plaice of the 1925 year-class in the Nissum Broad in the autumn of 1925 and the spring of 1926, the great invasion does not take place until the summer of 1926.

The fishermen's hauls consist almost exclusively of fish over 4 years old, the remainder being undersized. Out of 2252 plaice taken with Eel-Tog in 1926, only 16, or 0,7 %, were of retainable size.

B. The Inner Broads of the Limfjord. All taken in Eel-Tog.

	0-Group	I-Group	II-Group	III-Group	IV-Group	V-Group	VI-Group	Total investigated
No. of plaice in 1923:	3	218	74	89	66	20	2	472 spec.
» » » » 1924:	2	23	53	68	32	14	4	196 »
» » » » 1925:	10	18	78	76	11	9	»	202 »
» » » » 1926:	»	183	93	105	39	2	»	422 »

Expressed in %:

1923:	0,6	46,2	15,7	18,9	14,0	4,2	0,4
1924:	1,0	11,8	27,0	34,7	16,3	7,2	2,0
1925:	5,0	8,9	38,6	37,6	5,4	4,5	»
1926:	»	43,4	22,1	24,8	9,2	0,5	»

By the »inner broads of the Limfjord« I mean the waters between Oddesund and Løgstør. It is interesting to compare the distribution of the year-classes here

*) I have here disregarded the possibility of an emigration of older year-classes to the North Sea. The likelihood of this is to my mind very slight, but only marking experiments can determine the question with certainty.

with that for Nissum Broad; it must be borne in mind that the plaice here in the inner Limfjord waters originate from Nissum Broad, partly by natural immigration, partly by transplantation. As is only natural, we find the same year-classes dominant in both localities, viz. 1922, 1923 and 1925, the years 1921 and 1924 being but poorly represented in comparison. It is remarkable, by the way, that the I-Group in 1923 was especially numerous in the inner Limfjord, but relatively poor in Nissum Broad. This can hardly be explained otherwise than by supposing that great numbers of the I-Group must have migrated from Nissum Broad into the inner waters. The detailed lists show that this migration took place more especially in the course of the summer, and as these lists generally afford good information as to the movements of the plaice in these waters, I have reproduced them below. The figures indicate the catch per hour with Eel-Tog, and all values noted are therefore comparable.

		0-Group	I-Group	II-Group	III-Group	IV-Group	V-Group	VI-Group	Total	
1923	1'— 5' May		11,3	7,3	37,3	34,0	10,0	1,3	101,2	spec.
	10'—14' Sept.	1,5	100,5	31,5	16,5	7,5	2,5		160,0	»
1924	21'—24' May				48,0	17,0	9,0	2,0	76,0	»
	8'— 9' July			13,3	5,3	4,7	3,3	0,7	27,3	»
	7'—12' Sept.	1,6	17,9	25,7	9,4	6,2		0,8	61,6	»
1925	17'—23' May			8,7	32,7	7,6	8,7		57,7	»
	11'—16' Sept.	5,7	10,3	40,0	26,3	2,3	0,6		85,2	»
1926	17'—19' April		5,3	24,0	39,3	14,4	0,5		83,5	»
	14'—22' July		19,2	4,8	3,5	1,7	0,2		29,4	»
	22'—27' Sept.		48,0	12,0	4,0	0,6			64,6	»

The stock of plaice in the inner Limfjord thus consists, as we see from the table, of far younger fish in the autumn than in the spring of each year. This cannot be due to the fishery, as the most intensive fishery, viz. that with the seine, is only allowed during the period from 15th Sept. to 14th April, and would therefore rather act in the opposite direction. Nor can it be due to the transplantion operations, which, as we know, take place in April of each year; for the figures above quoted represent for the most part only those areas of the inner Limfjord where no transplantation takes place (the broads between Oddesund and Livø), these being the waters where the very great majority of the plaice were caught. The cause must therefore be looked for in an immigration of predominantly younger fish in the course of the summer half-year.

It will be noticed that some few of these plaice come in to the inner waters of the Limfjord while still in the 0-Group; this takes place in autumn, but only in the western broads, at Kaas and Venø. The great bulk of the immigrants

consist of I-Group and II-Group fish; and in particular, there has been an enormous immigration of the rich year-classes 1922 and 1925.

In addition to this immigration of young fish there is evidently also an emigration of older fish during the summer half-year. It will be seen from the tables that the number of plaice of the III-Group and IV-Group decreases considerably from spring to autumn in all years. On the other hand, the number of older fish will often, but not always, increase during the winter half-year; and this can hardly be explained save as an indication that the immigration of older fish during this season exceeds the depletion caused by fishery and emigration together.

We have then, in the western broads of the Limfjord, migrations of considerable extent among the plaice. It has long been known that periods with continued westerly wind and marked inflow of salt water from the west often lead to an immigration of plaice into the inner Limfjord broads; but there has been less occasion to observe any movements of the fish in the opposite direction, though these would of course be of the greatest importance to the fishery. In the table above, for instance, we notice that the number of 3—5—year—old fish, which form the principal constituent in the fishermen's hauls, dwindled in the course of 1926 almost to nothing; there can hardly be any doubt but that this has something to do with the remarkable poor yield of the plaice fishery in the autumn of 1926. Something of the same sort evidently took place in 1924, corresponding with the fact that the yield of the plaice fishery that year was less than both that of 1923 and that of 1925.

Studies on
The Biology of the Oyster *(Ostrea edulis)*.
II—IV.

By

R. SPÄRCK

CONTENTS.

		Page
	Preface	45
II.	The Feeding and Growth of the Pelagic Larvae of the Common Oyster *(Ostrea edulis)* .	46
III.	Some Observations of the Conditions of the Food Supply of the Common Oyster *(Ostrea edulis)*	56
IV.	On Fluctuations in the Oyster Stock in the Limfjord	60

PREFACE.

The following short papers form a kind of continuation of my previously published treatise on the biology of the oyster (Biol. Stat.'s Ber. 30). They contain some preliminary results of the investigations which I have carrried out on this subject during the last few years for the Danish Biological Station and which supplement those previously published. I am greatly indebted to Dr. phil. C. G. Joh. Petersen who was at that time Director of the Station, for his support and for the interest he has taken in my work. Professor Dr. phil. Aug. Krogh has also rendered me great assistance and has readily placed laboratory facilities at my disposal, while the Zoophysiological Laboratory provided me with the necessary funds for visiting the Norwegian oyster pools. My thanks are also due to Professor Dr. phil. Brinkmann for the exceedingly friendly help rendered to me during my visit to the oyster pools in Norway, likewise to Hr. K. Krohnstad, assistant to the Fishery Society of Bergen, who together with Professor Brinkmann accompanied me out to the oyster pools. I am also greatly indebted to Dr. phil. R. Ege for carrying out a series of analyses. Last but not least I must offer my thanks to Hr. Villars K. Lunn, Director of the Oyster Fishing Company, and to Lieutenant J. Lunn, who have both continually given me all possible support, have attended to my experiments during my absence from Nykøbing and in a number of ways have rendered me valuable help.

Copenhagen, January 1927.

R. Spärck.

II.

The Feeding and Growth of the Pelagic Larvae of the Common Oyster *(Ostrea edulis).*

While in literature on the American oyster a good deal of information is found on the biology of the larva, the corresponding particulars published up to the present concerning the common European species are exceedingly scarce. In an earlier work (Spärck 1924) I have given a summary of the the literature which had been published up to that time on the subject. At that time the only thing known about the biology of the larva of the common oyster was that the pelagic stage at 16°—20° C. lasted 8—14 days and that there appeared to be a connection between a high temperature of the water and a considerable number of larvae attaching themselves, which again according to the observations made could only be explained as a result of the high temperature of the water increasing the growth of the larvae, by reason of which the pelagic stage was shortened. Since 1924, so far as I know, only one paper dealing with the larvae of the common oyster has been published (Amemiya 1926). In this treatise it is shown that *Ostrea edulis* is not capable of propagation at a salinity under 24 per mille as segmentation at a lower salinity does not progress normally. Amemiya did not succeed however in getting the larvae of the *O. edulis* in the aquarium to develop beyond the very earliest stages whereas in the case of *O. virginica* this presented no difficulty. The cause of the difference in development between these two species of oyster must presumably be that Amemiya succeeded in finding a way of feeding the larvae of *O. virginica:* viz. with the flagellate *Pontosphœra huxleyi* which was approximately 5 μ in length. The feeding experiment with the larvae of *O. edulis* was, however, not equally succesful and on the whole the underlying reason for the extremely scanty results of all experiments with the common oyster larvae as well as of all breeding experiments on a larger scale seems to be the difficulties of feeding the larvae.

In recent years the hatching out of oysters in tanks has been attempted in various places, notably at Conway in Wales a long series of experiments have

been made in this direction. According to the preliminary reports which have come to hand up to the present date (Report on Sea Fisheries for 1919—23, 1924 and 1925) these experiments do not seem to have led to any method whereby reliable results can be obtained. In certain years very favourable results were obtained, whereas in other years under apparently similar conditions the results have been negative. The encouraging success which seemed at first to accompany the hatching out experiments in Conway led to similar experiments being begun in the Oyster Company's tanks on Ørodde near Nykøbing, Mors. If such experiments could led to positive results, the economic benefit to oyster fisheries would be immense, and especially so to Danish fisheries, where owing to climatic conditions it has proved impracticable to maintain any large fishery solely on its natural stock. But also for the fisheries of other countries a reliable method of hatching out would be of the utmost value. The experiments which the Oyster Company began in 1923, and which since 1924 have been taken up also by the Danish Biological Station, have given results no more positive than those obtained abroad. On the other hand a great deal of experience both of a positive and a negative character has been acquired through the experiments during these years, especially concerning the main problem of the whole question i. e. the feeding of the larvae, and it is for this reason that the following preliminary report seems to me to be justified.

I have already had occasion to describe shortly (Spärck 1924 p. 46) the first experiments which were undertaken in the summer of 1923. Ten tanks were employed, each containing about 150 cubic metres of water, the depth of water being a little more than 1 metre. Water was admitted to the tanks through an eleventh tank, being pumped into the latter from the Limfjord, and led out again from it to the experimental tanks in such a way, that it passed from the tank at the pump to tank No. 1, from this to No. 2 and so on; the water therefore which came to No. 10 had first passed through all the other tanks. In the middle of June mother oysters were laid out in the tanks; oysters from the Limfjord being employed, which had been dredged immediately before being placed in the tanks, as also Dutch oysters which had been left over from a consignment imported for sale in the previous winter. These latter had for some months lain in a tank in running water. 115—400 oysters were laid in each of the ten tanks, the majority being Dutch and being placed a little more closely than three to the square metre. The salinity in the tanks at the beginning of the experiments was approximately 30 per mille, the temperature, very low for the time of year, being about 12°—14° C.

At the beginning of July the temperature began to rise very rapidly; on July 5th it was about 17° C. in the tanks, in the afternoon of the next day 19.5° C. and from July 8th—17th between 20° and 23° C. On July 18th it began to fall and by the 22th it was down at 16° C. On July 5th the first oysters in the tank began to spawn and already by the 9th the density of the

larvae approximated to 1 per 10 cubic centimetres. When the fall in the temperature commenced, the number of larvae began to decrease very speedily, their density on July 22nd being approximately 1 per 1000 cubic centimetres. The free-swimming larvae had a length of 0.17—0.20 mm., two however being found on July 23rd of 0.26 mm. Further examination of the spat collectors in the tank (mussel shells, slate plates etc.) showed, that the larvae had not attached themselves anywhere, which is in accordance with the fact that no pelagic larvae had been observed of the size which must, according to Hagmeier's investigations (1916, p. 223), be expected, that they should have before attaching themselves. The mother oysters appeared to thrive on the whole, mortality was slight and in several cases there was observed a growth of about 1 cm. In the course of the first week or two there appeared in the tanks a considerable growth of micro-organisms, which was particularly noticeable in the warm period, both of diatoms, flagellates and other micro-organisms, as also of nematods and copepods (Harpactids). The salinity increased during the experiments to 31.5 per mille.

The result of this year's experiments was that when the temperature in the tank approached 20° C. there was no difficulty in obtaining an abundance of pelagic oyster larvae. On the other hand attempts at getting the larvae to grow to full size were not successful, since their growth ceased upon the commencement of a fall in the temperature, and consequently a method of keeping the temperature constant and fairly high had to be adopted the following year.

The experiments were now taken up also by the Biological Station, and Dr. C. G. Joh. Petersen, who was at that time director, obtained funds for installing two tanks, which could be kept at a constant temperature by artifical means. Over the two tanks, which with the water at its full height contained 30 odd cubic metres, was erected a wooden shed, which during the first two years' experiments had very small and few windows so that the light over the tanks was rather poor. The necessary heating arrangements consisted of a lead pipe which was led along the bottom round the periphery of the tanks and through which warm water passed at a temperature of 30°—40° C. By this method the water in the two tanks could be comparatively easily kept at a temperature of 20°—22° C.

In 1924 experiments were begun on May 20th. As it was feared that the larvae might experience difficulty in obtaining suitable food in sufficient quantity a low height of water was first employed (32 cm), so that this could if necessary be remedied later by pumping in fresh water. At the beginning of the experiment the salinity was 26.9 per mille, pH 8.2, the calcium content 0.36 mg. Ca per cubic centimetre. In each of the tanks were laid 120 mother oysters, which had been dredged immediately before in the fiord. The temperature was now raised very slowly in the tanks by heating, so that on July 20th it stood at 18°—20° C. It soon became clear however that the mother oysters experienced difficulty in obtaining their food, and this was only partially remedied by the addition of fresh

water to the one tank and of decaying zostera to the other. This brought about not only mortality among the oysters, but also a great delay in spawning, which in spite of the high temperature did not start until July 14th—15th. The mother oysters were now removed. In order to further improve the conditions of the food supply, water was siphoned out and new water pumped in daily; and in order to prevent the egress of the oyster larvae through the siphon, its mouth was covered with a filter of gauze, the distance between the meshes being 0.1 mm. It was found however in the course of a few days that the growth of the oyster larvae ceased, and after 10 days they were all dead, the bottom of the tanks being covered with their shells. No larva had attained a length of more than 0.20 mm. An attempt at improving the growth of the larvae by increasing the proportion of water renewed daily from $^1/_6$ to $^1/_3$ was unsuccessful, since it hastened their death to such an extent that they now only lived 3—4 days. The temperature was however successfully maintained at 18°—19° C. despite the considerable change of water. At certain intervals the concentration of hydrogen ions and the calcium content in the tanks were determined without any alteration however being observed; the salinity increased during the course of the experiments to approximately 28 per mille. The death of the larvae cannot accordingly be ascribed to these factors. To make certain that lead was not present in the water, an analysis was taken, but not the slightest trace could be found. The water was also tested for iron in view of the presence of some iron nails, but an analysis showed that the concentration was 0.000020 per cent., which is somewhat less than in the fiord, and therefore devoid of significance. The only explanation therefore that I can suggest of the death of the larvae is lack of food, since the constant pumping in of fresh water admitted a number of plankton organisms which must have competed with the oyster larvae for food. As the outflowing water was filtered the "concentration" of competing organisms became constantly stronger. The fact that the death of the larvae was hastened by the increased changing of the water seems to me also to indicate that this competition was the decisive factor. This view was further confirmed by the fact, that the larvae in the tanks which were neither heated nor covered grew better and attained a greater size than did those in the heated tanks. When the spat collectors laid out in the tanks were investigated in the autumn, it was found — as was to be expected — that no oysters had attached themselves, whereas the bottom and sides of all the tanks, both heated and unheated, were thickly covered with annelids, *Nereis diversicolor* and *Polydora ciliata* predominating; in the unheated were found in addition *Mytilus edulis, Cardium edule* and *Mya arenaria.* I can only explain this result, which I have previously reported (Spärck 1926 p. 278) by the hypothesis that among the plankton organisms which were the same in all tanks, the annelid larvae were the most successful in the struggle for food, and in the heated and covered tanks, where food conditions were bad on account of the poor light, and where the need of food by reason of the high temperature was greater, were accordingly the only

organisms capable of surviving the pelagic stage. In the uncovered tanks, a number of lamellibranch larvae were also successful in obtaining sufficient food, being however few in number compared with the annelids, although the number of the pelagic lamellibranch larvae differed only slightly from that of the pelagic annelid larvae. The oyster larvae on the other hand, who were among the most numerous of the pelagic organisms in the two categories of tanks, were nowhere capable of maintaining themselves. I came therefore to the conclusion that oyster larvae are particularly badly situated as regards competition for food. It follows from this that, so long as food is to be provided in such experiments solely by renewing the water, it will be necessary to filter the added water in order to avoid admitting with it plankton organisms that will compete with the oyster larvae for food. For technical reasons this could not be done in the summer of 1924, and some attempts at improving food conditions in the heated tanks by adding crushed green *Zostera* or bottom detritus (picked up by bottom sampler) did not lead to any result, not even to the slightest improvement in the growth of the larvae.

In the summer of 1925 a series of attempts at solving the question was carried out by the method of changing the water. It soon became clear that with any simple means (i. e. filtration through gauze) it was impracticable to obtain at the same time an effective filtration and a renewal of water in any considerable quantity, since either the filter gave way or the replenishment of the water took place too slowly; and finally it was extraordinarily difficult to obtain sufficiently fine filtration in this way. The results of these experiments also were thus entirely negative; the larvae died in the course of some days after growing a very little or not at all.

It was clear to me after the experiments in 1924 that there was scarcely any possibility of such experiments leading to a result, until it could be proved with certainty on what oyster larvae could be fed, and until this food could be supplied to the tanks in sufficient quantity.

Three kinds of food for the pelagic larvae of the *O. edulis* suggest themselves at the outset: micro-organisms, emulsified organic substances (detritus) and dissolved organic substances. In order to throw more light on these questions, a series of experiments was made at the close of the summer in the Zoophysiological Laboratory on feeding oyster larvae. The larvae for these experiments were caught with plankton nets in the tanks at Nykøbing and transported to Copenhagen in glass tubes which were put into a Thermos flask with ice. This proved to be the most satisfactory mode of transport; the larvae arrived in all cases alive and apparently full of vitality, and often lived for 14 days or longer. The sudden cooling from 18°—20° C. to 0° C. and the following rewarming to 18°—20° C. appeared to have no direct noticeable effect on the larvae.

The motive of the experiments was to induce the larvae to grow in various nutrient solutions as also in emulsions and cultures of micro-organisms. As nutrient

solutions were employed a) a 0.1 per cent. solution of glucose, b) solutions of albumen and predigested meat (in concentrations of 0.1, 0.3 and 0.01 per cent.), and c) a nutrient preparation, bioklein. The choice of the last was due to the publications of Krizenecky (1924 p. 187) in which he suggests that amphibian larvae can be fed on solutions. Despite many variations in the conditions of the experiments which were carried out in large and small jars, with and without aeration, in the light and in darkness, and at various temperatures (11°—21° C.) the results were entirely negative. The larvae experimented upon lived in some cases for 8—10 days, but no growth was observed, and in a control experiment with sea water passed through a centrifuge they lived just as long or longer. There appeared to be no difference in the effect of the various solutions apart from the fact, that the larvae lived on an average longer in the weakest concentrations. A trial with a number of emulsions (milk, yolks of eggs, egg albumen, alkaline albuminate, alkaline casein, finely chopped up *Zostera*) gave similar results. The larvae lived no longer in the emulsions than in the pure water of the control experiments and no growth was observed. Finally a number of experiments were undertaken in feeding the larvae with cultures of *Nitzschia minutissima* which Dr. Allen of Plymouth kindly sent us. The result was once more negative, and it could be observed directly under the microscope that these organisms were too large to be absorbed by the oyster larvae. The conclusion cannot of course be drawn from the failure of these experiments that the feeding methods thus tried are not practicable under certain conditions, but they did on the other hand prove that a simple addition of these solutions and emulsions is not sufficient. As regards *Nitzschia* culture it may be said that the negative result is beyond doubt.

The striking contrast between the speed of growth and the vitality of the larvae in the covered in tanks on the one hand and in the non-covered in tanks on the other must lead to the inference that the supply of food depended on the presence of green organisms. Judging from the experience with *Nitzschia* however, these organisms must be very small, of size category 2—3 μ. Meanwhile Professor Krogh had drawn my attention to the plankton filter described by Kolkwitz (1924 p. 205) by means of which several cubic centimetres of water can be filtered in the course of a comparatively short time, through filters with pores as small as $^1/_2$ μ. In the early summer of 1925 I filtered a quantity of water from the Limfjord and therein a number of uni-celled green organisms on which the larvae probably fed out in the fiord. In order to throw light on this question and altogether to solve the problem of the conditions of the food supply of the oyster larvae, I paid a visit in July 1925 to the Norwegian oyster pools. In these pools we have up to the present the only instance of a really considerable number of oyster larvae growing up and attaching themselves in a comparatively limited quantity of water, at a very high temperature too. For this to take place there must necessarily be present very abundant food in the water of these pools, so

that one might suppose that it would be easier there to come to some definite conclusion on the question.

When I visited the pools (the Espevik and Selø pools in the outer Hardanger Fjord, the Inderø and Selvaagen pools farther to the North) the temperature in the pools was 25°—31° C., and in the plankton were found a number of oyster larvae only comparatively few however having the full size for attaching themselves. In the Espevik pool some larvae were seen about 0.30 mm. in length. In the plankton were found besides quite a number of other lamelllibranch larvae, presumably *Modiolaria marmorata*, of which there were enormous numbers in the pools. By filtering the water through the Kolkwitz filter it was found that the micro-organisms were present in much greater numbers than in the Limfjord, including *Prorocentrum micans* together with various green algae, among which was a little micro-organism closely allied to, or possibly identical with the little uni-celled green algae observed in the Limfjord. There was as mentioned above a considerably greater number of micro-organisms than in the Limfjord, but they were of a far lower size category than I had expected. This may perhaps explain the comparatively small number of large oyster larvae. Consistent with this is the fact that oysters in the Espevik pool attached themselves in that year in very small numbers, only a thousand or two indeed, as I was informed later by the assistant Hr. Krohnstad.

It was very striking that passing the water in the pools through a centrifuge produced no demonstrable quantity of detritus, and my observations greatly strengthened my view that oyster larvae fed on the above mentioned small organisms. This view was to be confirmed from many quarters in the following year. In January 1926 we received a communication from Conway to the effect that oysters had, in the summer of 1925, attached themselves in some numbers in the tanks where the water had contained small green algae, presumably a *Chlorella*. In September the results of some experiments with lamellibranch larvae were published by Kändler (1926), which show that they can easily be fed on "eine marine Protococcide", size 3—4 μ. By the kindness of Dr. Dodgson I obtained through the agency of Dr. C. G. Joh. Petersen some samples of water from the tanks in Conway, whereupon it was found that the *Chlorella* mentioned above was identical with, or at least closely allied to, the uni-celled green algae observed by me in the Limfjord and in the Norwegian oyster pools. Finally my view was confirmed by tank experiments in the Limfjord.

Before these were commenced, I had in the spring of 1926 carried out a series of experiments with a view to finding out what conditions were required for a considerable growth of this micro-organism to take place. These experiments were carried out in the orchid house of the Botanical Gardens in order to obtain adequate light and heat, and I am greatly indebted to the director Professor Ostenfeld for granting me these facilities. The experiments proved that the green algae in question required firstly, much light, secondly a high temperature.

It was consequently quite impossible to obtain a growth of any significance until the end of March, since till then the light had not been adequate. Cultures placed in the corners of an ordinary room gave equally negative results. In windows or in the orchid house on the other hand a considerable growth took place. These experiments proved further that the growth in ordinary Limfjord water was very slight and in some cases amounted to nil, whereas water to which had been added the nutrient salts employed by Dr. Allen for diatom culture, or still better water with a rich content of organic matter gave a far more satisfactory growth. In water with a content of organic matter corresponding to 300—400 c. c. of kalium permanganate per litre (i. e. 6—8 times as much as the highest figure in ordinary Limfjord water) at a temperature of about 25° C. it was found possible in the course of 10 days to increase the density of a *Chlorella* culture from 8 per cubic millimetre to 1,800, and in 3 weeks to 10,000. With a lower temperature (about 10° C.) the density increased in 3 weeks from 8 per cubic millimetre to 1,500. As regards nutrient solutions which were prepared from the salts employed by Allen and Nelson (1910 p. 428) the corresponding figures after 10 days at a temperature of 25° C. were 700 per cubic millimetre, after 3 weeks at about 10° C. 500 per cubic millimetre. A 100 per cent. increase in the degree of concentration of the salt gave a somewhat increased density, a further increase on the other hand was unsuccessful.

The methods employed to produce the high content of organic matter were firstly, to let dead oysters and lamellibranchs remain in the water and completely decompose, secondly, in accordance with the advice of Dr. phil. Boysen Jensen to add urine in a concentration of 1 c. c. to the litre. A series of experiments on the other hand with ordinary sterilized Limfjord water produced, as mentioned above, only a very slight growth and consequently low figures of density of *Chlorella*. The greatest success was experienced when the water had stood for some time, owing presumably to the ensuing pollution of the water. These culture experiments with *Chlorella* prove therefore that the conditions requisite for its growth are particularly favourable in water containing an abundance of organic matter. I consider that this fact contributes in a high degree to the understanding of conditions in the Norwegian pools. These latter have very stagnant water, the temperature is high, and at the bottom there is often advanced decay. Most often they are surrounded by forests and abundant vegetation, and the presence of a considerable content of organic matter is therefore of course to be expected in the water of the pools. An analysis of a sample from the Espevik pool was taken which showed the content of organic matter to be in a proportion of 120 c. c. of kalium permanganate per litre, which is rather more than twice the proportion in ordinary Limfjord water. It is certainly this content of organic matter, perhaps in conjunction with nutrient salts washed out from the surrounding soil, which makes possible such a great production of nutrient organisms in the pools, that up to half a million oyster larvae can at times live and attach themselves in so

little water as that contained in the Espevik pool. When in certain years, despite a satisfactory temperature, oysters do not attach themselves to any great extent, this is probably due to the fluctuations in the production of the micro-organisms on which the oyster larvae are to feed. It is possible that the presence of other larvae which compete with these for food may be a factor of some importance; the bad result in 1925 can perhaps be explained by the presence alone of great numbers of other lamellibranch larvae in the plankton.

With the experience gained in these experiments with *Chlorella* – whereby it proved possible to obtain considerable quantities of practically pure cultures of this organism — it was clear that the requirements for the 1926 experiments would be firstly, to provide light for the tanks and secondly, to provide an adequate content of organic matter in the tank water. A glass roof was therefore put on to the shed which stands over the experimental tanks; whereby an additional advantage was gained, namely that artificial heating could as a rule be dispensed with. In order to obtain a suitable content of organic matter one tank was prepared as follows: in April after the tanks had been filled with water, a layer of old *Zostera* was put on the bottom, the whole tank being covered over with a tarpaulin in order to avoid a too extensive growth of the organisms. The tank was now left for two months, in which time the content of organic matter was nearly quadrupled. To the other tank liquid manure was added shortly before the beginning of the experiment, but only in the proportion of $^1/_2$ c. c. per litre, in order to avoid a too great production of bacteria. This brought about a fivefold increase in the content of organic matter, in that its content before the addition was made was considerably lower than the maximum values found in the Limfjord (the proportion at the beginning being only 25 c. c. of kalium permanganate per litre).

In July mother oysters were laid in these tanks. Spawning took place very quickly, whereupon *Chlorella* cultures were added in such quantities as to produce a density of the organisms approximating to 8 per cubic millimetre. An extensive growth took place in the tanks, and especially in the one to which liquid manure had been added, not only of *Chlorella,* but also of other organisms, viz. diatoms (chiefly *Nitzschia),* flagellates, large uni-celled green algae, *Phormidium,* bacteria etc., also of a number of marine animals, especially nematods and copepods (Harpactids). This had an obviously bad effect on the growth of the oyster larvae which however was remedied to no slight extent, at any rate as regards the growth of bacteria, by changing the water to the moderate extent of one tenth of the total volume daily, which took place freely without the filtration presenting any difficulty.

The result of the experiment was therefore that the larvae in both tanks not only grew in 1926 in contrast to preceding years, but grew at the rate which was to be expected in view of the temperature (approximately 20° C.). The number decreased steadily it is true but some thousands reached in the course of 10 days very nearly that size at which attachment takes place. Several larvae were observed

which were over 0.30 mm in length and had distinct anlage of feet. In several cases it was observed directly under the microscope that the larvae consumed *Chlorella*.

Despite the fact that the possibility of oysters attaching themselves was by no means precluded this year, yet upon draining the tanks in the autumn nothing was found. With a view to the possibility of larvae having attached themselves the quantity of water changed daily was increased. One or two which were found on old oysters originated probably from the larvae in the tank, but they cannot be regarded as an adequate basis for forming any conjectures. The fact that, despite the satisfactory growth of the larvae, no large number of oysters had attached themselves can presumably be explained by the conditions of the food supply not having been good enough notwithstanding the food supply the measures taken, whether this was due to the presence of too many other organisms or to the growth of bacteria having been too great. It is clear that food conditions must be exceptionally good if any high percentage of attachment is to be looked for. The number of small oysters that were fished up in the years immediately following 1914, when it may be assumed that the whole oyster stock in the fiord had spawned, show that the attachment even in that particularly favourable year took place in the approximate proportion of one attached oyster to every million of pelagic larvae and that only under favourable conditions. It is clear therefore that quite exceptionally good conditions are requisite if this percentage is to be raised. In itself an attachment of 2—3 larvae in the experiments described above where we had only a few hundred thousand larvae (the mother oysters were removed as soon as spawning commenced) would have been no slight result in comparison with conditions in the fiord.

Even if the experiments thus failed to give any result as regards the attachment of larvae, I am nevertheless of the opinion that they have this year advanced considerably our knowledge of the conditions of the food supply of oyster larvae. We have also thereby gained such a basis for future experiments that a positive result cannot be said to lie outside the limits of possibility. And even if results of practical importance with regard to hatching out on a large scale should not be obtained, a good deal of information will in any case be gained concerning the biology of oyster larvae, and this again may be of great importance to us as regards our comprehension of the biology of the oyster living under natural conditions.

The results of the experiments may be finally summarized as follows:

1. When the temperature approximates to 18°—20° C. and the mother oyster is adequately fed, there is no difficulty in getting oysters to spawn even in quite small tanks. If the oyster has been badly fed, spawning does not take place or at least is considerably delayed.

2. Oyster larvae in comparison with annelid larvae and the other lamellibranch larvae must be looked upon as particularly difficult to feed. This explains the extraordinarily infrequent attachment (1 : 1,000,000) in oyster beds under natural

conditions even in favourable years. On the other hand, even great fluctuations in temperature have no direct influence on the vitality of the larvae.

3. It has been demonstrated by experiment and observation that oyster larvae can be fed on uni-celled green algae of size category 3 μ.

4. These micro-organisms seem to multiply rapidly, particularly when the temperature is high and the water contains a considerable amount of organic matter. The great production of oysters in certain years in Norwegian pools is probably due to this, as well as to the peculiar hydrographical conditions. There is undoubtedly a partial connection between the fluctuations in the production of oysters and the fluctuations in the growth of micro-organisms. It will doubtless be found possible to take steps in this connection and "dung" the oyster pools in the same way as is done in the freshwater fishponds.

III.

Some Observations on the Conditions of the Food Supply of the Common Oyster *(Ostrea edulis)*.

During the experiments described in the foregoing section and also during my visit to the oyster pools in Norway, I have further had the opportunity of making some observations on the feeding of adult oysters. The observations made during the experiments in the tanks have been in part published previously (Spärck 1926 a). These observations had already slightly modified my view on the conditions of the food supply of oysters, and this modification has been confirmed to some extent by the publications on this theme which have appeared since 1924. In my first work on the biology of the oyster (1924 p. 70) I set forth certain observations on the conditions of the food supply of the common oyster and added to these some comments. At that time our knowledge of the more detailed anatomy of the alimentary canal of the oyster and of its digestive processes was very slight. The view commonly held on the conditions of the food supply of oysters rested therefore exclusively on examination of stomach contents, obviously a somewhat slender basis so long as it is unknown how much of the stomach contents is actually ingested and digested. As it appeared from the examination of stomach contents that finely divided particles of organic matter (detritus) were quantitatively predominant, it was a natural deduction that detritus must constitute the chief part of the food of oysters. This hypothesis was asserted also during the years 1903—4 and right up to 1920 by a number of investigators such as Rauschenplat, Lohmann, C. G. Joh. Petersen, Blegvad and others, and it must be admitted that such a view was quite justifiable, when one takes into consideration the data then available and and the material collected for obser-

vation. In the above mentioned publication I was able, merely on the strength of the examination of several hundred stomach and intestine contents, to confirm the fact that in the contents of the intestinal canal of the oysters from the Limfjord detritus was quantitatively predominant. Also by means of a direct experiment I proved to my satisfaction that an addition of »artificial detritus« to an aquarium containing oysters brought about a demonstrable improvement in their food, mainly by a reformation of the crystalline style (ibid. p. 71). It is true that I was not then aware of the presence of such small organisms as the *Chlorella* which was described in the foregoing section, but the aquarium stood in a very dark room where the temperature was 10° C.—15° C., so no great growth of such micro-organisms could have taken place. On the basis of these observations I came of necessity to the conclusion that vegetable detritus played an important part in the feeding of oysters. It is true that I made one single observation in the opposite direction, finding, as I did in the embanked Klovvig where extraordinary conditions prevailed in respect to the composition of plankton, that the stomach contents of the oysters consisted exclusively of *Prorocentrum micans*.

During the above mentioned tank experiments it appeared however that is was not the detritus food that played a great part but that, as I have previously described (1926a p. 271—75), the oysters fed on green organisms, especially flagellates, or derived their food from an admixture of glucose to the water in the tank, benefiting however in the latter case presumably from the indirect effect of the excessive growth of bacteria thereby produced.

The stomach contents of the oysters in the Norwegian pools consisted exclusively of organisms, mainly *Prorocentrum micans*, but also numerous smaller green planktonic algae and flagellates. This is perfectly consistent with the fact that the water when passed through a centrifuge showed no detritus in demonstrable quantities, whereas filtration through the Kolkwitz plankton filter showed no slight density of such organisms. These observations prove that the oyster under certain circumstances is able to live almost exclusively on micro-organisms and this seems even to be the rule so far as small quantities of stagnant water are concerned. It would certainly be impossible by any other method than through a great production of green organisms to obtain a sufficient production of food in small quantities of water.

Two further works have appeared since 1924 as mentioned above which to a considerable degree have constributed to our knowledge respecting the condition of oyster food, viz. the papers by Vonk and Yonge, which were published in 1924 and 1926 respectively. Vonk's work deals especially with the presence, previously demonstrated by List, of phagocytes in the cells of the tubules of the digestive diverticula in *Mytilus*. Vonk succeeded in showing that oysters are able similarly to ingest by means of phagocytes fine particles in the epithelial cells of the tubules, and one may assume that this is quite common among the lamellibranchs. Vonk has further carried out the experiment of feeding oysters

in aquaria with plankton with the result that they, in contrast to unfed control oysters, had distinctly green contents in the epithelium of the tubules of the digestive diverticula, which must have originated from the added samples of plankton. Vonk seeks to explain that the green cell contents originate from diatoms although he admits that there are certain difficulties in the way. As, however, no more accurate analysis of the plankton samples exists, and as attention has not been directed to quite small organisms such as were mentioned in the foregoing section, it is extremely probable that these green cell contents have had some origin other than from diatoms.

This entire problem is now gone into more deeply in Yonge's treatise. It commences with a detailed description of the anatomy of the alimentary canal and of the histology of the oyster, concerning which, as I have mentioned, only the most scanty information was available, derived as it was mainly from Hoek's work in 1881. After a very close description of the ciliary currents both on the gills and in the palps as also in the intestinal canal, the author describes very closely the digestive process itself and the absorption of food. Here also will be found a mass of new and valuable information. Firstly there is demonstrated the presence of freely moving phagocytes in the intestinal canal, and it is shown that these are capable of ingesting *Nitzschia*. The fact that the epithelial cells of the digestive diverticula are able to exercise a phagocytic function, in that they are capable of ingesting lesser insoluble particles, is also corroborated, and this investigation thus provides us with the necessary histological and physiological basis for comprehending the oyster's faculty of feeding on micro-organisms. In the final section Yonge describes the conditions of the food supply in general and attacks the detritus theory put forward by Blegvad (1914) and other Danish investigators. Since Yonge maintains that he has proved that the oyster lacks enzymes for the digesting of pentosans, which latter according to Boysen Jensen (1914) constitute a considerable part of the detritus in the sea, he looks upon detritus as being of no, or in any case of subsidiary, importance as a source of food. I cannot see that this view is justified, for even if the oyster is not able to digest detritus by means of enzymes, there is nothing to prevent this being done with the help of micro-organisms. Something of this kind appears to be the case as far as all insects are concerned which feed on cellulose, and it may be regarded at the outset as improbable that the great quantities of organic matter, which in the form of detritus are brought by the water into the intestine of the oyster and most other lamellibranchs, and which often forms a very considerable part of the intestine contents of these animals, should not be accessible to them. The experiment mentioned above and previously published by me points also in this direction. But this question will scarcely be capable of solution until we have obtained more accurate knowledge of the bacteria and other micro-organisms that live in the intestinal canal of the oyster.

Concerning the third possible food source, i. e. dissolved substances, we have

extremely little information relative to oysters. Mitchell (1915 p. 153) has shown that *O. virginica*, when kept in a 0.25 per cent. solution of glucose acquires an increasing content of glycogen and fat. I myself have made a couple of experiments with *O. edulis* and have obtained a somewhat similar result. 8 oysters were put into an aquarium containing 8 litres of water and glucose was dissolved in it so as to form a solution of 0.043 per mille. After one day the proportion of glucose had sunk to 0.022 per mille, and after two days the sugar had practically disappeared, in that the proportion was now only 0.004 per mille. A corresponding experiment was made with saccharose; in the course of two days the water in the aquarium had sunk from 0.063 to 0.0015 per mille. A control experiment with oyster shells in the tank showed that most of the sugar content must have been absorbed by the oysters. No information extists, so far as is known to me, concerning the feeding of oysters by this method and consequently nothing further can be said at present regarding its practicability.

Our present knowledge of the conditions of the food supply of oysters may thus be summarized as follows:

1. The investigations of Vonk and Yonge in the laboratory together with the observations set forth here from the oyster pools in Norway and the experiments in the Limfjord tanks prove conclusively that oysters can feed exclusively on micro-organisms. *Prorocentrum micans*, small flagellates, and uni-celled green organisms seem to play here a predominant part. In certain localities, especially in small quantities of stagnant water, they seem to be the only, or at least the predominant food of the oyster.

2. It cannot at present be demonstrated with certainty to what extent and degree detritus is of importance, since no information is to hand concerning the part played by micro-organisms, especially bacteria, in their capacity as a possible intermediate link. The great frequency with which detritus is found in the intestine contents of oysters in most waters, as also the experience gained from a single experiment, make it appear probable however that detritus is of importance, in any case indirectly.

3. Certain experiments indicate that solutions may also be of some importance.

4. Whereas some knowledge thus exists regarding the qualitative side of the food question, we have practically no information regarding the quantitative side of the problem.

IV.

On Fluctuations in the Oyster Stock in the Limfjord.

We have two means of judging the size of the oyster stock in the Limfjord; firstly, the yield of the fishery, secondly, the two experiments carried out by divers who were sent down to get an idea of the size of the stock by direct counting. The first method must of course be employed with caution, seing that the fishing methods used at different times do not always give figures of yields from which comparisons can be safely instituted. Nor can the method by direct counting give any great accuracy; it will however be quite sufficient to give a rough idea of the conditions, especially as regards showing in what direction development is taking place. The yield of the fishery can also give a rough idea of the size of the stock and especially of its fluctuations, particularly since the method introduced in 1910 of calculating the number of oysters fished per boat per day.

In my first treatise on the biology of the oyster (1924 p. 48) I have sought to prove, that the great decrease in the yield of the oyster fishery at the close of the seventies of the last century took place after a series of cool summers, as did the decrease after 1922, whereas the great yield of the fishery during the years 1910—1920 followed after a series of comparatively warm summers. In other words I sought to prove, that there is a certain periodicity in the yield of the fishery: i. e. that good periods alternate with bad ones and that the fluctuations coincide with changes in climatic conditions and are presumably caused by them.

Since then, Hagmeier (1926 p. 11) has published a survey of the yield of the West Sleswig oyster fishery from the year 1859. It appears that the fluctuations in the Sleswig fishery coincide completely with those in the Limfjord fishery. At the close of the sixties the yields of both fisheries were on the increase; the yield of the West Sleswig fishery culminated in 1869—70 with $5^1/_2$ million fished up oysters, that of the Limfjord fishery in 1871—72 with $7^1/_2$ million. From that time a marked decrease began for both fisheries, and in 1881—82 the annual yield of the Sleswig fishery had sunk to 470,000 where upon a ten years close time was instituted. The yield of the Limfjord fishery had in 1895—86 decreased to 920,000 per annum, and a close time was here similarly instituted (until 1890). After the close time it was found that the stock had not increased appreciably; in the nineties and at the beginning of the present century the yield of the Sleswig fishery lay round about 300,—400,000 per annum; the yield of the Limfjord fishery was at that period slightly on the increase and after 1900 reached the figure of about 1 million. During the period 1910—20 the yields of both fisheries were on the increase, the Sleswig fishery yielding 750,—850,000 per annum, and the Limfjord fishery 3—4 million culminating in 1915—16 with $5^1/_2$ million. In the years 1922—23 a very great decrease took

place in the yields of both fisheries; in 1924—25 the annual yield of the Sleswig fishery had sunk to 118,000 and that of the Limfjord fishery to 500,000, whereupon both fisheries closed down.

Such a close agreement between the yield of the oyster fishery off the west coast of Sleswig and that of the Limfjord can in my opinion only be explained by the fact that a common factor, i. e. the climate, plays a great part in determining the size of the stock and accordingly the yield of the fishery. I can therefore only look upon this as a confirmation of the theory put forward above that the climate, due mainly to the influence of the summer temperature on spawning and on the rate of growth of the larvae, is a very important, probably the most important of all the factors which determine the fluctuations in the size of the oyster stock.

But apart from the influence which is in this way exerted on the reproduction and thereby on the size of the stock, there are other factors which exert influence here, and amongst the most important of them are those which regulate the annual decrease in the stock. Here the two chief factors are the fishery and the natural mortality. I have previously (ibid. p. 78) estimated the latter to be about 20 per cent. per annum of the stock. In recent years we have obtained various data which seem to show that this figure is if anything rather too low than too high. Firstly the diving investigations in the summer of 1924 (Rep. Dan. Biolog. Stat. 32. p. 15) showed that the mortality in the severe winter of 1923—24 had been considerably higher, probably about 50 per cent. for the fiord taken as a whole, although there was a marked variation in the different parts of it. Finally we have obtained from the fishery of recent years on the beds with relaid oysters no slight data for estimating mortality. Here also we find a marked variation in the percentage of mortality both from year to year and from place to place. If we take the percentage of mortality from the 23 beds with relaid oysters which have been fished over during the years 1915—25, we find figures that lie between 10 and 38 per cent. per annum; in 7 cases the annual percentage was 20—25, in 3 cases over 30 (for more detailed statistics see "Fiskeriberetningerne" for 1920 and 1925). These variations seem to have been determined partly by time and partly by place.

If we take the percentage of winter mortality compiled from the data provided by the investigations by divers in 1924, it is perfectly obvious that the mortality in the abnormally cold winter of 1923—24 was lowest (about 20 per cent.) in the higher parts of the fiord (Venø Bay, Risgaard Broad, and Skive Fiord) i. e. in those parts where the ice covering lasts longest. We find the highest rate of winter mortality (about 70 per cent.) in Livø Broad, where there is a very low temperature in conjunction with open water, whereas Nissum Broad, where the temperature does not sink so low, has a much lower rate of mortality (30—40 per cent.). This seems to me to show that the cause of the high rate of winter mortality is not lack of oxygen due to the covering of ice but is due to the

severe cooling of the water, whereby ice crystals are, I think, formed in the adductor muscle of the oysters; this again causes a paralysis of the muscle so that in most cases sooner or later death ensues. Whereas we thus can explain the local variations in winter mortality by the cooling of the water in the winter, we are less able to explain the summer mortality and its causes. We have here partly a variation from year to year, in that the mortality on the beds with relaid oysters in Nissum Broad has been particularly high in certain years, especially in the years following 1922, and partly a variation from place to place so that the mortality has often been different in localities very close to one another. In three of the beds with relaid oysters which were laid out in the spring of 1926 the mortality in the summer of 1926 was only about 10 per cent. while in the fourth it was about 25 per cent. All the beds lie along the north coast of Nissum Broad, the one on which mortality is greatest, in the corner within (East of) the Mullergrund. This peculiar difference might be explained by the hypothesis that presumably by reason of the situation the water in the last mentioned oyster bed has been renewed to a much less extent than the water in the other beds and that the higher mortality is thus due to bad conditions of food supply. When one considers that the oyster at a higher temperature is likely to experience food difficulties (Spärck 1926 a.) it will not appear antecedently improbable that bad conditions of food supply can be one of the reasons for this peculiar local summer mortality. As far as the variations from year to year in summer mortality are concerned, I have previously (Spärck 1926 b. p. 7) put forward the hypothesis that this mortality after 1922 was due to a continuous accumulation of predaceous animals and competitors for food, as oysters had been laid out for a long series of years in a very limited area along the north coast of Nissum Broad and off Lemvig Røn. This hypothesis is confirmed by Hagmeier (1926 p. 7) who lays particular stress on the rapid growth of Bryozoa, Ascidia, and Hydroids as well as of the great masses of *Asterias rubens* and *Carcinus maenas* in some of the West Sleswig beds. With reference to Nissum Broad there is especial reason to notice *Ascidiella aspersa* which in certain years occur in huge masses in summer and can completely overgrow the oyster, thus greatly obstructing its access to food and water.

We thus see that if we estimate the annual mortality among oysters in the Limfjord at about 20 per cent. we are by no means taking too high a figure; it is even considerably greater for certain years and in certain localities. Mortality falls into two categories: firstly winter mortality which is limited to certain abnormally cold winters, and which appears to be due to an excessive cooling of the water, seeing that it is not met with in localities where the water is covered with ice for long periods, and secondly summer mortality. Much seems to point to the belief that the latter is due to food difficulties, the encroachment of predaceous animals and the like.

How great an influence fishing has had on the variations in the stock can

only be estimated when the precise size of the stock is known. According to the investigations by divers which have been carried out up till now (C. G. Joh. Petersen 1908 and 1925) the stock has been estimated at about 100 million in 1907, 5—10 million in 1924. It we take the yield per boat per day as a basis for an estimate this has sunk during the period 1910—1924 from 3000 odd to about 500, i. e. to $^1/_6$, whereas according to the diving investigations the stock has sunk to $^1/_{10}$—$^1/_{20}$. As the investigations by divers in 1924 are based on 47 trials, against 16 in 1907, it is probably best to regard the figure arrived at in 1924 as the most accurate, the figure arrived at in 1907 being probably too high. Even if one however estimates the size of the stock during the period 1910—1920 to have been 50 million, and it can scarcely have been less, it is clear that the fishing which for most years has yielded about 3—4 million has not brought about a diminution of more than 6—7 per cent. of the stock, i. e. a comparatively small figure compared with the 20 per cent. for which annual mortality is responsible.

Finally there is still one question that I must touch on in a few words: To what extent has the size and density of the stock an effect upon reproduction?

It may be regarded at the outset as probable that this effect is only slight. However, certain facts seem to me to indicate the contrary. It is for instance distinctly remarkable that in recent years far fewer young oysters in proportion to marketable oysters have been dredged than was the case some years ago, although the temperature in the summer months had by no means been unfavourable; in fact in the summers of 1925 and 1926 it was even considerably more favourable that in all the other years since 1914. In 1920—21 the young oysters still constituted about 25 per cent of all the fished up oysters, in 1924—25 only 5 per cent.

It was also remarkable that after the warm summer of 1926 practically no small oysters could be found in Livø Broad, whilst in several places in Nissum Broad, where there lay several million relaid Dutch oysters, quite a number of the 0-group were found. This seems to me to indicate that the question of the density of the stock is by no means devoid of significance in reference to reproduction. It might indicate that the stock can become so numerically weak and dispersed that reproduction even under favourable circumstances may be very slight. It is quite true that this is in contrast to what experience with a number of small lamellibranchs seem to show, where even a quite small number are capable of renewing the stock. The explanation is presumably that eggs of *O. edulis* are fertilized in the reproductive organs or mantle cavity of the mother animal, whereas among most of the small lamellibranchs fertilization takes place in the water, where the distance between the separate animals consequently plays a much less important part.

Our knowledge of the fluctuations in the stock in the Limfjord may be accordingly summarized as follows:

1. A comparison between the yields of the Limfjord and the Sleswig oyster fisheries confirms the theory that the climate (summer temperature) is the most

weighty factor. It is this that determines the good and bad periods extending over several years. Its influence is constant over a large area.

2. The next most important factor is natural mortality. This may be estimated at at least 20 per cent. per annum. In contrast to the first mentioned factor its effect varies greatly from place to place. Among the causes must be particarly emphasized the severe cold in conjunction with open water as regards winter mortality, and presumably food difficulties, predaceous animals, overgrowth by competitors for food and the like as regards summer mortality.

3. Diminution due to fishing may probably be taken to play a lesser part, as a rule accounting for about 8 per cent. of stock annually.

4. It is likely that the density of the stock influences reproduction to some extent.

BIBLIOGRAPHY

E. J. Allen & E. W. Nelson, 1910: On the artificial Culture of Marine Plankton Organisms (Journ. mar. biol. Ass. N. S. 8.) Plymouth.

I. Amemiya, 1926: Notes on Experiments on the early developmental Stages of the Portuguese, American and English Native Oysters, with special Reference to the Effect of varying Salinity (Ibid. N. S. 14.) Plymouth.

H. Blegvad, 1914: Food and Conditions of Nourishment among the Communities of Invertebrate Animals found on or in the Sea Bottom in Danish Waters. (Rept. Dan. Biol. Stat., 22.) Copenhagen.

P. Boysen Jensen, 1914: Studies concerning the Organic Matter of the Sea Bottom. (Ibid. 22. p. 1). Copenhagen.

A. Hagmeier, 1916: Ueber die Fortpflanzung der Auster und die fiskalischen Austernbänke. (Wiss. Meeresunters. N. F. Abt. Helgoland. 11.) Kiel & Lpz.

— , 1926: Ueber Austernkultur an Deutschlands Küste und die Bewirtschaftung der preussischen fiskalischen Austernbänke. (Mitt. deutsch. Seefischerei-Ver. 42.). Berlin.

R. Kändler, 1926: Muschellarven aus dem Helgoländer Plankton. (Wiss. Meeresunter. N. F. Abt. Helgoland. 16.). Kiel & Lpz.

R. Kolkwitz, 1924: Plankton-Membranfilter. (Ber. d. deutsch. Bot. Gesell. 42.) Berlin.

J. Krizenecky, 1924: Experimentelle Untersuchungen zur Frage nach der Ernährung der Wassertiere durch gelöste Nährstoffe (Zool. Anz. 48.). Lpz.

Th. List, 1902: Die Mytiliden des Golfes von Neapel. (Fauna & Flora d. Golfes v. Neapel. 27.). Berlin.

P. H. Mitchell, 1916: Nutrition of Oysters. (Bull. U. S. Bur. Fish. 35.) Washt.

C. G. Joh. Petersen, 1908: Studies on the Oyster and the Oyster Fisheries in the Limfjord. (Rept. Dan. Biol. Stat. 17.). Copenhagen.

— , 1925: Investigations concerning the Size of the Oyster Stock in the Limfjord 1924. (Ibid. 31.). Copenhagen.

R. Spärck, 1924: Studies on the Biology of the Oyster (Ostrea edulis) in the Limfjord. with special Reference to the Influence of Temperature on the Sex Change (Ibid. 30.). Copenhagen.

» , 1926 a: Zoogeography in Relation to Marine Biology. (Physiol. Papers ded. Prof. Aug. Krogh). Copenhagen.

» , 1926 b: Beretning om Østersfiskeriet i Limfjorden i de 5 Sæsoner 1920/21—1924/25. (Fiskeriber. f. 1925.). Kjbhvn.

H. J. Vonk, 1924: Verdauungsphagocytose bei den Austern. (Zeitschr. f. vergl. Physiologie. 1.). Berlin.

C. M. Yonge, 1926: Structure and Physiology of the Organs of Feeding and Digestion in Ostrea edulis. (Journ. mar. biol. Ass. N. S. 14.). Plymouth.

XVII. *C. G. Joh. Petersen*: II. Second Report on the Oyster and Oyster Fisheries in the Lim Fjord. 1908. (24 pp.)

XVIII. *The same*: I. The Yield of the Limfjord fisheries in recent years and the transplantation of Plaice in 1908. With 6 tables and 1 Chart. II. Biological investigations on the stock of Plaice in the Limfjord. With 3 Tables. III. The Yield of the Prawn fishery from 1885—1907 and its improvement by means of protection. With 3 Tables. 25 pp. 1909.

XIX. *The same*: Some Experiments on the Possibility of combating the harmful Animals of the Fisheries, especially the Whelks in the Limfjord. 20 pp. 1911.

XX. *C. G. Joh. Petersen and P. Boysen Jensen*: Valuation of the Sea. I. Animal Life of the Sea-Bottom, its food and quantity. With 6 Tables, 3 Charts and 6 Plates. 81 pp. 1911.

XXI. *C. G. Joh. Petersen*: Valuation of the Sea. II. The Animal Communities of the Sea Bottom and their importance for marine Zoogeography. With 6 Plates, 3 Charts and an Appendix. 110 pp. 1913.

XXII. I. *P. Boysen Jensen*: Studies concerning the organic matter of the Sea Bottom. II. *H. Blegvad*: Food and Conditions of Nourishment among the Communities of invertebrate animals found on or in the sea bottom in Danish waters. III. *C. G. Joh. Petersen*: The Work of the Biological Station from 1889—1914. With Illustrations and Tables. 88 pp. IV. *The same*: Appendix to Report XXI. With 2 Charts. 7 pp. On the distribution of the Animal Communities on the Sea Bottom. 1914.

XXIII. *C. G. Joh. Petersen*: On the Animal Communities of the Sea Bottom in the Skagerak, the Christiania Fjord and the Danish waters. With one Chart and four Tables. 29 pp. 1915.

XXIV. I. *C. G. Joh. Petersen*: On the Development of our Common Gobies *(Gobius)* from the Egg to the Adult Stages etc. With 1 Plate and 3 Figures in Text. II. *H. Blegvad*: On the Food of Fish in the Danish Waters within The Skaw. 72 pp. 1916.

XXV. *C. G. Joh. Petersen*: The Sea Bottom and its production of Fish-food. A survey of the work done in connection with valuation of the Danish waters from 1883—1917. With 12 Plates and 1 Chart. 82 pp. 1918.

XXVI. I. *P. Boysen Jensen*: Valuation of the Limfjord. I. Studies on the Fish-Food in the Limfjord 1909—1917, its Quantity, Variation and Annual Production. With 7 Plates and 1 Chart. II. *C. G. Joh. Petersen*: Our Gobies (Gobiidæ). From the Egg to the Adult Stages. With 3 Plates. 65 pp. 1919.

XXVII. *C. G. Joh. Petersen*: On the stock of Plaice in relation to the intensive fishing of the present times in the Beltsea and other waters. With 2 Plates. 21 pp. 1920.

XXVIII. *H. Blegvad*: On the Biology of some Danish Gammarids and Mysids. *(Gammarus locusta, Mysis flexuosa, Mysis neglecta, Mysis inermis.)* With 5 Tables. 102 pp. 1922.

XXIX. *C. G. Joh. Petersen*: On the Stock of Plaice and the Plaice Fisheries in different Waters. With 2 Charts and 1 Appendix. 42 pp. 1922.

XXX. *R. Spärck*: Studies on the Biology of the Oyster (*Ostrea edulis*) in the Limfjord, with special Reference to the Influence of Temperature on the Sex Change. 80 pp. 1925.

XXXI. I. *C. G. Joh. Petersen*: The Influence of Fishing upon the Stock of Plaice in the Baltic during recent Years. — II. *R. Spärck*: Investigations on the Size of the Stock of Oysters in the Limfjord 1924. — III. *C. G. Joh. Petersen*: Report to the Ministry of Agriculture concerning increased Motor-Fishing in the Limfjord. — IV. *H. Blegvad*: Continued Studies on the Quantity of Fish-Food in the Sea Bottom. — V. *R. Spärck*: A Comparison between the Danish Oyster-Beds and those in Holland and the South-West of France. 63 pp. 1925.

XXXII. *H. Blegvad:* On the Renewal of the Stock of Plaice in the Baltic proper. 37 pp. 1927.